

A computational study of emergent phenomena in Vicsek-like models

*Flocking, cooperation and competition of
active particles*

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Abstract

This thesis is a numerical study of the emergence of collective behavior and pattern formation from the movement of self-propelled particles. They can interact either directly through self-alignment or indirectly through chemotaxis. Flocking is when organisms move in synchrony through directional alignment with their nearest neighbors and without leadership. The Vicsek model is commonly used to study flocking. Two alterations of it will be studied. The first incorporates game-theory approaches, allowing particles to adopt cooperative or defecting strategies. The second introduces interactions based on spring forces and a combination of alignment and anti-alignment between particles. In addition, indirect interactions based on the nutrient gradient and the chemical signal gradient will be examined.

Sammendrag

Denne oppgaven er en numerisk studie av hvordan kollektiv atferd og mønsterdannelse kan oppstå i systemer bestående av selvdrevne partikler. Disse partiklene kan påvirke hverandre enten direkte ved å orientere seg etter hverandre, eller indirekte gjennom kjemotakse. Flokkatferd oppstår når organismer beveger seg synkront ved å la seg påvirke av orienteringen til andre organismer i nærheten, uten å ha en leder. Vicsek modellen benyttes ofte for å studere slik atferd. To varianter av Vicsek-modellen vil bli undersøkt. Den første varianten er inspirert av spillteori. For hver partikkel fins det to mulige strategier: å samarbeide eller å lav være å samarbeide. Den andre modellen inneholder partikler som orienterer seg i samme eller motsatt retning. De påvirker også hverandre gjennom fjør krefter. I tillegg vil en model hvor partikler påvirker hverandre indirekte bli studert. Her skjer påvirkningen gjennom næringsgradienter og kjemiske signalgradienter.

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Chapter 1

Introduction

This thesis explores different migration and interaction strategies of binary systems of active (self-propelled) particles to better understand the emergent collective behavior in such systems. Collective behavior refers to the behavior of a system that emerges due to many interacting individuals following simple rules.

Biological organisms have evolved diverse strategies to navigate their environments and adapt to varying conditions. One notable strategy is flocking behavior, characterized by groups moving translationally in synchrony without a designated leader. This phenomenon has been observed in numerous organisms, including starlings[12], locusts[11], and bacteria [13].

Studying flocks is important for several reasons. For instance, studying locust swarms may give insight into how to better protect crops from them [2]. On a cellular level, flocking models can help explain various collective migration processes such as embryonic development, wound healing, and the formation of vascular networks [20]. From a physics perspective, flocking is fascinating because it allows for analogies with classical systems like liquids and gases [29]. Moreover, a flock is an example of a system with synchronization, which is a widely studied topic in physics.

Reynolds recognized in 1987 that flocking can be understood in terms of three principles, avoidance, attraction, and alignment[25]. Avoidance refers to the fact that individuals will try to avoid collisions. Attraction refers to the tendency for individuals to move towards each other. Lastly, alignment refers to the individual's tendency to move in the same direction as individuals nearby. One can implement these principles through force based simulations of self-propelled particles. The avoidance and attraction can be modeled with forces that are repulsive at short range and attractive at long range. Spring force is an example of such a force. The alignment can be modeled through dipole interactions. The Vicsek model is a widely used model for flocking. It only uses the alignment principle. In the Vicsek model particles align their orientations by using the average orientation of their nearest neighbors. A brief introduction of the Vicsek model is presented in Chapter 2.

One question that I pursue in this thesis is the nature of alignment

interaction for a binary system of self-propelled particles. This situation might represent prey-predator dynamics or, more generally, two species of interacting particles. I focus on two specific types of alignment interactions: i) alignment strategies based on a game-theory approach; ii) alignment based on a weighted average of flocking versus anti-flocking tendencies.

A recent study from [34] has incorporated game theory into the Vicsek model. The particles had two strategies: cooperate and defect. There is a benefit (gain) with having high local order and a cost (loss) associated with cooperating. In Chapter 3, I present numerical results for different flocking regimes and corresponding phase diagrams, based on two final system states: one where only cooperators remain, and another where only defectors remain.

Another means of interaction among self-propelled particles is through spring-like forces. These forces can be used to implement attraction and avoidance as already mentioned. It has been shown by [14] how spring-like forces could cause flocking in a system of self-propelled particles. I have formalized a weighted Vicsek model with spring forces. A special case of this model, containing the two types red and blue, has been examined. Particles of the same type tend to align, while particles of different types tend to anti-align. In chapter 4, I discuss the emergence of clusters consisting of a red part and a blue part that rotate due to torque induced by self-propulsion.

Self-propulsion involves the conversion of chemical energy derived from nutrients in the environment into kinetic energy for translational motion. Therefore, it is important to study the nature of indirect interactions among self-propelled particles through nutrient gradients and chemical signaling in their shared environment. In Chapter 5, I address this foundational question through a minimal model of chemotaxis, similar to that proposed by [15]. I study different regimes of dynamic pattern formation and collective behaviors of particles across various model parameters, including nutrient diffusivity, self-propulsion speed, and the decay rate of the chemical signal.

In Chapter 6, I provide a summary discussion and conclusion.

Chapter 2

Flocking behavior

In this chapter, a minimal model that reproduces the flocking behavior seen across many biological systems will be presented. Vicsek introduced it in 1995 [31]. The model will be presented in 2 dimensions, and the flocking transition as a function of model parameters will be discussed.

2.1 Vicsek model

In the Vicsek model, the particles have two variables the position $\vec{r}$ and the orientation θ . The particles move at constant velocity v_0 . The positions get updated as:

$$\vec{r}_j(t+1) = \vec{r}_j(t) + v_0 \hat{n}(\theta_j(t)) \quad (2.1)$$

Here, v_0 is the velocity. $\hat{n}$ Is a unit vector. The orientation gets updated as:

$$\theta_j(t+1) = \tan^{-1}\left(\frac{\sin(\theta_j(t) + \sum_{n \in \Gamma_j(t)} \sin(\theta_n(t)))}{\cos(\theta_j(t) + \sum_{n \in \Gamma_j(t)} \cos(\theta_n(t)))}\right) + \Delta\theta \quad (2.2)$$

The first term is the average direction in the neighborhood. The first term is the average direction in the neighborhood. The set of neighbors is Γ_j , which is defined as all particles within a distance R from particle j . This can be mathematically defined as:

$$n \in \Gamma_j(t) \Leftrightarrow ||\vec{r}_j(t) - \vec{r}_n(t)|| < R \wedge n \neq j \quad (2.3)$$

The last term in Equation 2.2 is the noise. $\Delta\theta$ Is a number drawn from a uniform distribution in the range $[-\eta, \eta]$. If $\eta = \pi$, then all orientations are equally probable.

To analyze how synchronous the particles are, one often uses the order parameter, defined as:

$$\psi = \frac{\sqrt{(\sum_{j=0}^{N-1} \cos(\theta_j))^2 + (\sum_{j=0}^{N-1} \sin(\theta_j))^2}}{N} \quad (2.4)$$

Here, N is the total number of particles. This order parameter is the absolute value of the average velocity divided by v_0 . $\psi = 1$ Means that all particles are moving in the same direction. While $\psi = 0$ means that the particles all move in different directions.

v_0	R	η	N	L
0.1	2	0.5	499	31.6

Table 2.1: Parameters for the Vicsek model, N is the number of particles L is the domain size.

2.2 Numerical details and results

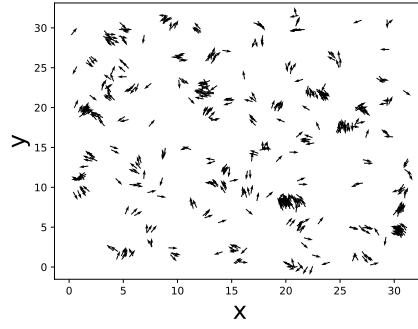
Results from simulations of the Vicsek model will now be shown. The simulations have been initialized by placing the particles randomly on a $L * L$ square with random orientations. Periodic boundary conditions have been used, such that the particles are always on a $L * L$ square. If a parameter is not specified, it will be given in table 2.1.

Figures 2.1, 2.2 and 2.3 show quiver plots for different radii. One can see that $R = 0.5$ gives many small clusters that each seem to move independently. This state is reminiscent of a gas. For $R = 2$ there is a lot more synchronous motion. Here, the particles seem to all move in the same general direction. It seems possible to draw streamlines for these plots, so the flow may be described as laminar. The number of clusters is small. For $R = 5$, all the particles seem to move in the same direction in one large system spanning cluster. One can therefore say that there is laminar flow here. Figure 2.4 shows the corresponding order. One can see that $R = 0.5$ gives low order, which makes sense since there are many clusters that seem to move independently. The order also fluctuates a lot. One can see that the order for $R = 2$ stabilizes more quickly. The order gets close to one, and it fluctuates a bit. For $R = 5$ the order stabilizes almost immediately. And the fluctuations are small, which makes sense since all particles in the quiver plots seem to move in the same direction. There seems to be two distinct phases. One where the system consist of many small clusters that each move independently. And another where all particles move collectively in the same direction. These two phases would have an order of zero and one, respectively.

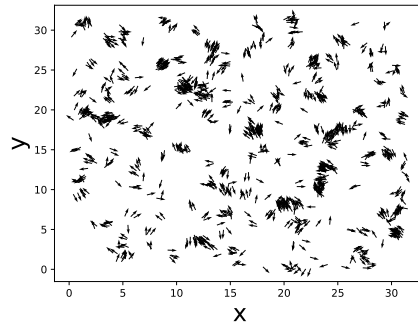
Figure 2.5 illustrates how the order parameter depends on R and η . To generate the η plot, 50 values of η were sampled uniformly in the range $[0, \pi]$. For each value, 20 simulations were run, each consisting of 1000 iterations. The order parameter was then averaged over the final 200 iterations and across all simulations. The R -dependent results were obtained using the same procedure, except with 5 simulations per value of R .

The order seems to be close to 1 for low η . It approaches 0 for high η . This indicates a phase transition between $\eta = 0$ and $\eta = \pi$. One may try to explain the plot by thinking in terms of two particles. Imagine that they are neighbors for one iteration. After that iteration, their orientations will be similar. In subsequent iterations, they will not be neighbors, and the difference in orientation will increase due to the accumulation of noise. Their orientations will become similar when they meet again. The order will therefore depend on how often they meet and how fast the noise accumulates, which depends on η . The maximum difference in orientation

$t = 100$



$t = 200$



$t = 300$

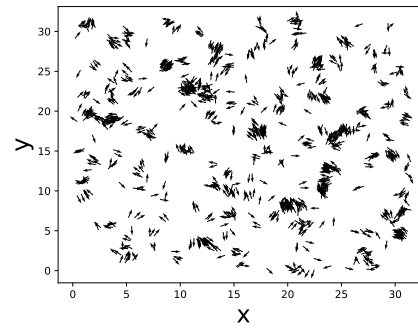
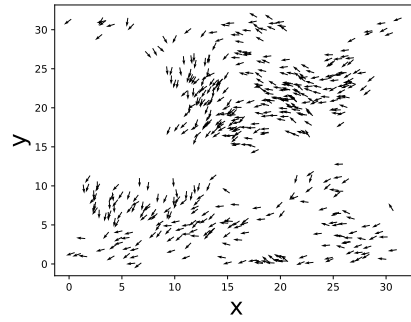
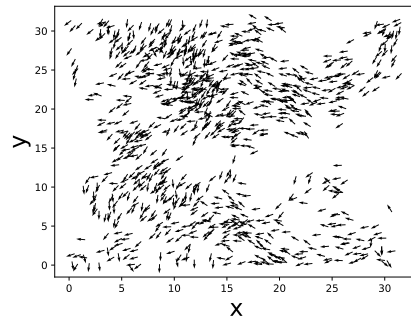


Figure 2.1: Snapshots of the system at different times for $R = 0.5$, showing the formation of small flocks.

$t = 100$



$t = 200$



$t = 300$

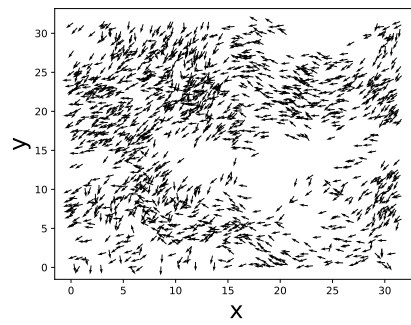
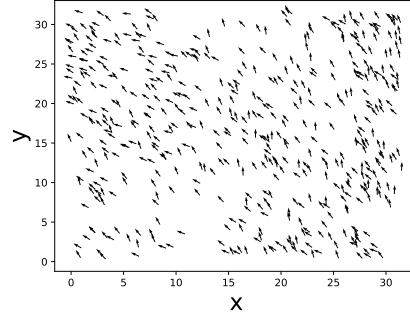
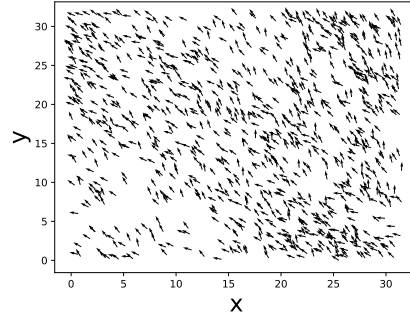


Figure 2.2: Intermediate flocks for $R = 2$. Snapshots at different times.

$t = 100$



$t = 200$



$t = 300$

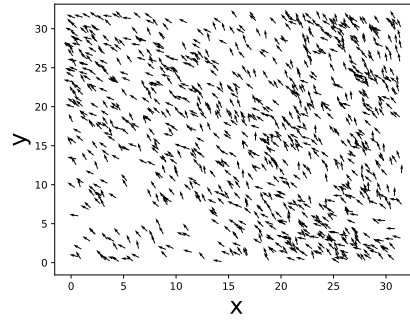


Figure 2.3: System-spanning flocks for large interacting radius. Snapshots of flocking states at different times.

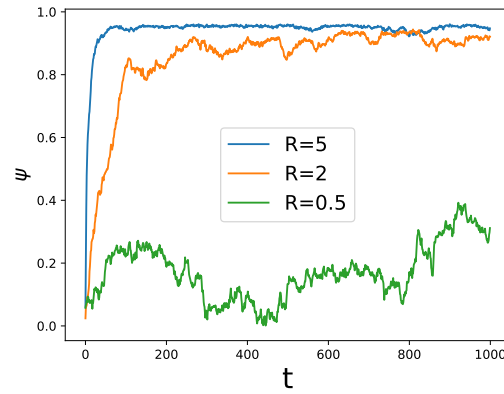


Figure 2.4: Flocking order parameter as function of time for different interaction radii $R = 0.5, 2, 5$.

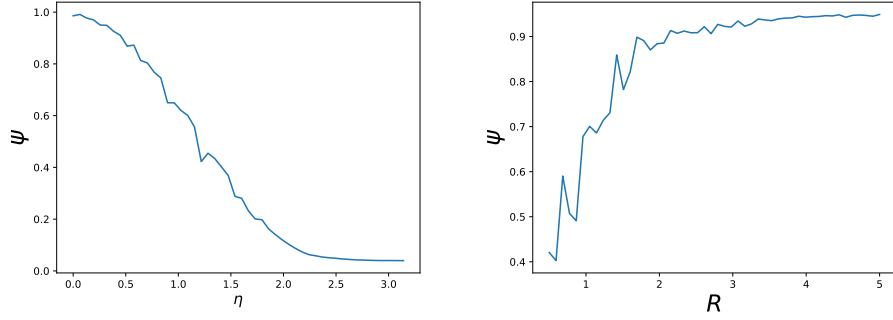


Figure 2.5: Flocking parameter in the statistical steady state. Plotted against the noise η and the interaction radius R .

the particles can have is π . Therefore, there might be a critical η when the number of iterations between each meeting is enough to make the difference in the orientations close to π .

In the R plot, the order increases dramatically from a 0 at $R = 0$ to nearly 1 at $R = 3$. When $R = 0$, the particles do not interact at all, so the order becomes 0. For small R , the system has many small clusters that move independently; therefore, there would be a small order. For large R there are more particles in each neighborhood contributing to a large order. In addition, the time it would take for a particle to leave a neighborhood would be larger. This would also lead to a large order.

2.3 Conclusion

In the Vicsek model, particles move at a constant speed and update their orientation by averaging the orientation vectors of their neighbors, with the addition of noise. The Vicsek model is characterized using an order parameter, which is the absolute value of the average orientation vector.

The Vicsek model has two phases. In one phase, the particles move in individual clusters that move independently. In the second phase all particles move in approximately the same direction. The order parameter can be used to characterize these two phases. When it is zero, it corresponds to the first, and when it is one, it corresponds to the second phase.

The flocking behavior seen in the Vicsek model resembles the flocking behavior of different animals. The two phases can help explain why some species form small clusters and others form large.

The models in the next two chapters have been inspired by the Vicsek model.

Chapter 3

Vicsek model combined with game theory

This chapter presents a modified Vicsek model, originally proposed by You in 2023 [34]. In this model, each particle adopts one of two strategies: cooperation or defection. Cooperative particles align their orientation with nearby neighbors, following the regular Vicsek dynamics, while defectors move in random directions. Each particle receives a reward based on the degree of alignment with its neighbors. In addition, cooperators receive a cost proportional to their neighborhood radius. Each particle updates its strategy by comparing payments with neighbors. The evolution of the system is explored under varying neighborhood radii. Depending on the parameters, the system exhibits two distinct phases: one where all particles eventually become cooperators, and another where all become defectors. Phase plots are used to illustrate how the choices of parameters dictate the outcome.

3.1 Introduction

Cooperation occurs in many biological systems. Examples include cleaner fish that remove parasites from other fish [16] and predators that hunt in packs. Cooperation often comes at a cost, raising the question of how it can evolve and be sustained. There is ongoing research aimed at identifying the conditions under which cooperation emerges.

Prisoner's Dilemma is a game commonly used to study cooperation. There are two players and two strategies: defect and cooperate. The payoff in the form presented by Nowak [21] is given in Table 3.1. This structure shows that it is better for both to cooperate than for both to defect. It also shows the potential benefit of defecting.

In [21], a model was introduced where this game was played on a square lattice. Each player updates its strategy by adopting the strategy of the player with the largest payoff. The model gave rise to a variety of spatial structures.

A similar formalism was applied to the Vicsek model by Chen [7]. Here, each particle moved in accordance with the Vicsek model, while playing

	C	D
C	(1, 1)	(0, b)
D	(b, 0)	(0, 0)

Table 3.1: Payoff matrix for the Prisoner's Dilemma. The first number is the payoff for the row player, and the second is for the column player. b is the benefit of defecting.

the same type of game with its neighbors and updating the strategy using a similar method. The strategies did not effect the motion.

Flocking can be viewed as a form of cooperation. There can be many benefits from flocking, such as the sharing of information [18] and predator avoidance [8]. There might be a cost to flocking. This cost could be the energy required to observe the neighbors. It can also be the case that the individual has to choose between flocking and moving towards a potential resource. Another potential cost of flocking is the risk of an infectious disease.

In [34], cooperation and defection was introduced into the Vicsek model in a way that was different from [7]. Cooperation meant that the particles would flock, and defecting meant that they would not flock. The model had a payoff where the gain was based on the local order, and the cost came from cooperating. To update the strategies, each particle compared its payoff with a random neighbor. It then made a stochastic decision on whether or not to adopt it. The use of stochastic decision-making accounted for irrational choices.

3.2 The model

The modified Vicsek model describes each particle with three variables: its orientation θ_j , the position r_j , and the strategy $s_j \in \{0, 1\}$. The particles move in a square domain of size $L * L$ with periodic boundary conditions, and their positions are updated according to Equation 2.1.

If $s_j = 1$, the particle is a cooperator, then θ_j gets updated using Equation 2.2, just like the regular Vicsek model. If $s_j = 0$, the particle is a defector and its orientation θ_j gets drawn from a uniform distribution over $[-\pi, \pi]$, effectively ignoring its neighbors.

The payoff of j is defined accordingly:

$$P_j(t) = Q_j(t) - c_j(t) \quad (3.1)$$

Here, Q_j measures the local order (benefit) and c_j is the cost. The cost is defined as:

$$c_j(t) = s_j(t) \alpha \frac{R}{L} \quad (3.2)$$

Here, R is the radius of the neighborhood. α Represents the relative cost. It determines how much R affects the cost. There is no cost for defecting. The

local order Q_j is defined according to the following sum:

$$Q_j(t) = \frac{\sum_{l \in \Gamma_j(t)} Q_{jl}}{|\Gamma_j(t)|} \quad (3.3)$$

Here Q_{jl} is the order between j and l which defined as:

$$Q_{jl} = \frac{||\hat{n}(\theta_j) + \hat{n}(\theta_l)||}{2} = \cos\left(\frac{\theta_j - \theta_l}{2}\right) \quad (3.4)$$

Q_{jl} Is the order parameter from the regular Vicsek model computed for l and j .

To update the strategy, j compares its payoff with a random neighbor l . j Then adopts l strategy with a probability given by the Boltzmann distribution. The Boltzmann factor for changing the strategy is $e^{\frac{P_l}{\beta}}$. While the Boltzmann factor for keeping the strategy is $e^{\frac{P_j}{\beta}}$. Therefore, the partition function for this system becomes:

$$Z = e^{\frac{P_j}{\beta}} + e^{\frac{P_l}{\beta}} \quad (3.5)$$

Which leads to the following probability for changing the strategy.

$$W(s_j \rightarrow s_l) = \frac{e^{\frac{P_l}{\beta}}}{e^{\frac{P_j}{\beta}} + e^{\frac{P_l}{\beta}}} = \frac{1}{1 + e^{\frac{P_j - P_l}{\beta}}} \quad (3.6)$$

This form of the Boltzmann distribution is known as the Fermi function. β Is the irrationality parameter. For high β $W(s_j \rightarrow s_l) = \frac{1}{2}$. And for low β , $W(s_j \rightarrow s_l) = 1$ if $P_l > P_j$, and 0 otherwise. The algorithm for the model is given step by step below.

Algorithm 1 Algorithm for the modified Vicsek model

```
procedure
  Choose the parameters  $v_0, \eta, r, L, N, \alpha$ , and  $\beta$ .
  Choose the initial conditions for  $N$  particles.
  Choose the number of iterations.
  for each iteration do
    for each particle  $j$  do
      Update position using Equation 2.1.
      if  $s_j(t) = 1$  then
        Update the orientation using Equation 2.2.
      else
        Draw the orientation  $\theta_j$  from a uniform distribution within
        the range  $[-\pi, \pi]$ .
      end if
      if there are neighbors then
        Pick a random neighbor  $l$ .
        Calculate the payoff of  $j$  and  $l$  using equation 3.1.
        With the probability given by Equation 3.6,  $s_j(t+1) =$ 
 $s_l(t)$ , otherwise  $s_j(t+1) = s_j(t)$ .
      else
         $s_j(t+1) = s_j(t)$ 
      end if
    end for
  end for
end procedure
```

3.3 Method and Results

To do the simulations, I have initialized the system by placing the particles randomly on a $L \times L$ square. Their initial orientations have been drawn from a $[-\pi, \pi]$ distribution. Half of the particles have been designated as cooperators, and the other half as defectors. Unless otherwise specified, the parameters I used are listed in Table 3.2. See [27] for the link to the GitHub repository with the code.

v_0	η	r	L	ρ	α	β
0.1	0.5	2	31.6	0.5	1	1

Table 3.2: If I have not specified the value of a parameter, its value will be given in this table. ρ Is the density.

I started by recreating the results seen in Figure 1 a, b, and c from [34]. Here, they have made plots of the order and fraction of cooperators for the radii 0.2, 2, and 8. They used a density of $\rho = 1$. They averaged over 50 simulations. I have not used averaging. The result from my

replication can be seen in Figure 3.2. Figure 3.1 contains quiver plots from the corresponding simulations. Animations corresponding to this have been included in the GitHub repository.

From the plots in figures 3.2 and 3.1, one can see that the system will eventually end up with only defectors or cooperators. Once the system has ended up with only cooperators, it behaves as the regular Vicsek model. The order is very small for $R = 0.2$. However, the system ends up with cooperators, since there is a small cost caused by the small radius. For $R = 2$, the system first experiences a growth in the number of cooperators. Then, as a consequence, the order increases. For $R = 8$ the order increases rapidly in the beginning due to the large radius. The large radius also implies a large cost, which leads to an increase in the number of defectors. At some point, there are so many defectors that the growth in order stops. Then the defectors make the order decline. This causes an increased growth in the number of defectors. This leads to reduced order, which again causes an increase in the defector growth. So there is a feedback, which eventually leads to the system ending up with only defectors and zero order.

I want to find the conditions that determine whether the system will eventually end up with all cooperators or all defectors. Therefore, I have made phase plots. In figure 3.3, the phase has been plotted in α η space. Here, each point represents one simulation. I have used 20 values for α in the range $[0, 4]$ and 20 values for η in the range $[0, \frac{\pi}{2}]$. The simulations were given a maximum of 2000 iterations. Once the average value of s reached 0 or 1, the simulations stopped.

Large η implies smaller order. Therefore, one can see that the α separating the cooperating and defecting phase becomes smaller with increasing η . The boundary almost seems linear. Near the boundary the probability of ending up in either phase becomes close to equal. This leads to an unsharp boundary. To remedy this, I could have used more simulations for each point, and then let the state that won in the majority of the cases determine the phase. We may refer to the values that lie along the boundary between the two phases as critical.

The critical η at $\alpha = 0$ seems to be the same for all the radii. This value of α implies that there is no cost for cooperating. And the reason for there being defectors is only due to the stochastic decision-making. For high η , the local order for cooperators becomes close to 0. Therefore, the probability for a cooperator to adopt a defector's strategy after comparing becomes close to $\frac{1}{2}$. If the irrationality parameter β was smaller, the critical value for η when $\alpha = 0$ would be larger. If I had used enough simulations and let the most frequent state represent the phase, the critical value for η would be π . Since this value would imply zero order and therefore equal probability for either outcome.

For critical values of η , one expects that the difference in payoff between the cooperators and defectors becomes close to zero. Based on the fact that the critical η seemed the same for all the radii, one may assume that the local order does not depend on R . This leads to the following relation for

the critical regime:

$$0 = Q_c(\eta) - \alpha \frac{R}{L} - Q_D(\eta) \quad (3.7)$$

Here, Q_c is the local order of a cooperator and Q_D is the local order of a defector. One can then write:

$$\alpha = \frac{k(\eta)}{R} \quad (3.8)$$

Where $k(\eta)$ is:

$$k(\eta) = (Q_c(\eta) - Q_D(\eta))L \quad (3.9)$$

To test this, I have tried to find the critical value of α when $\eta = 0$ from the plots in Figure 3.3. To do this, I have used visual inspection. I then went on to use least squares to fit equation 3.8 to the data. The result is seen in Figure 3.5. The curve seems to roughly fit the points. I got $k = 4.79$.

I have also made phase plots in α, R space. Using the same method that I used in the η and α case. The result is seen in Figure 3.4. In the case where $\eta = 0$, I have plotted the curve from Figure 3.5 in the phase plot. The curve seems to roughly fit the boundary. The boundaries in the other α, r phase plots seem to show the same type of curves. One can see that a larger η leads to a smaller region for the cooperator phase. This is again caused by η creating less order.

3.4 Conclusion

The model described in [34] is a modified Vicsek model, with two strategies. The strategies are cooperation and defection. The cooperators update their orientation in accordance with the regular Vicsek model. The defectors updated their orientation by choosing a random angle. The particles update their strategy by comparing their payoff with a random neighbor. The payoff is the difference between the local order and the cost of cooperating.

The system will eventually end up with all defectors or all cooperators. Phase plots have been made based on these states. The border between the cooperating states and defecting states looked roughly linear in the phase plots with noise and relative cost. For the plots with interaction radius and relative cost, it looked like a hyperbola. For future analysis, one could make equivalent plots for the probability of ending up in the cooperator phase. This would provide more information.

This model may help predict the conditions that are necessary for flocking to evolve in a species. In the Vicsek model flocking does not occur if the noise is too large or the interaction radius too small. Adding cost to the Vicsek model provides an alternative explanation for why flocking does not occur.

An interesting alteration of the model would be to use open boundary conditions. For periodic boundaries, the defectors and cooperators are forced to interact. This causes the system to end up with either defectors or cooperators. With open boundary conditions, the cooperators could escape

the influence of the defectors. This could lead to a system that ends up with a mixture of cooperators and defectors. This might be used to explain the spatial distribution of a species.

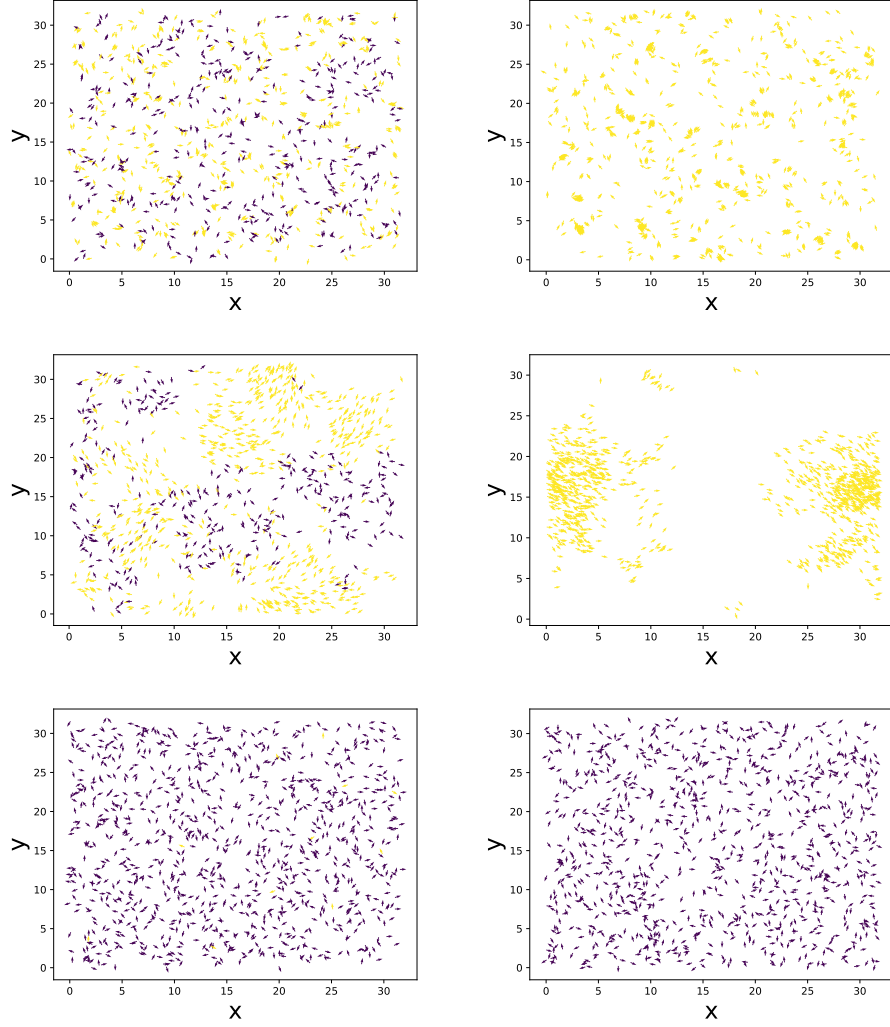
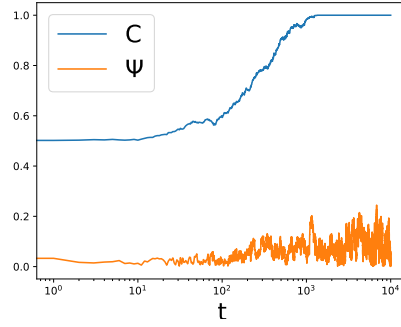
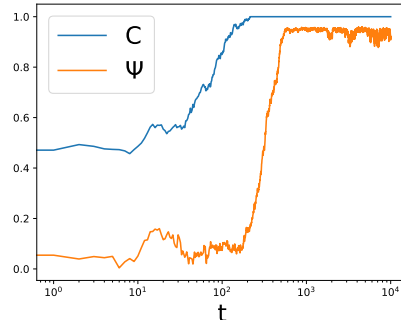


Figure 3.1: Quiver plots from simulations when $\rho = 1$. The left column is at step 50 and the right is at step 9999. At the top row $R = 0.2$, at the middle row $R = 2$ and at the bottom row $R = 8$. The blue arrow represents the defectors and the yellow arrows represent the cooperators.

$R = 0.2$



$R = 2$



$R = 8$

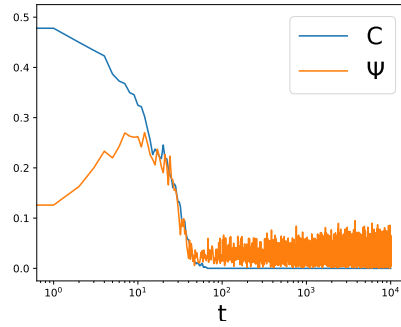
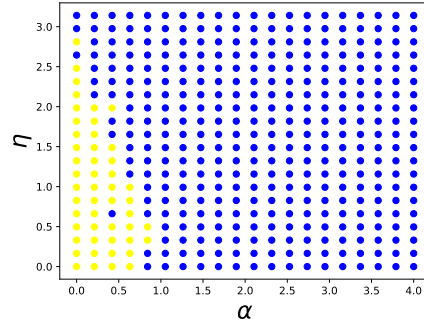
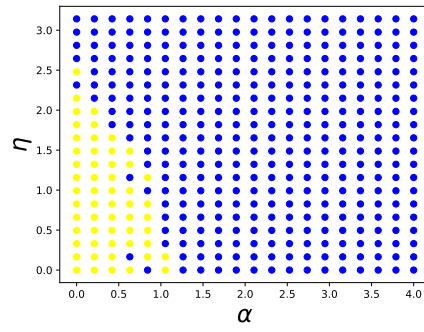


Figure 3.2: Plots showing how the order Ψ and fraction of cooperators C evolve with the iterations. The density is $\rho = 1$.

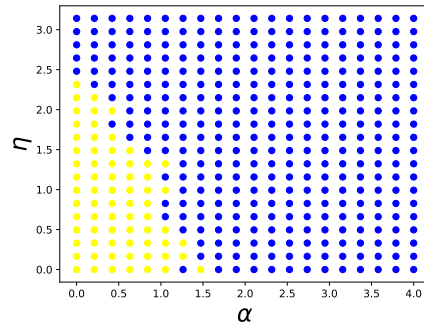
$R = 5$



$R = 4$



$R = 3$



$R = 2$

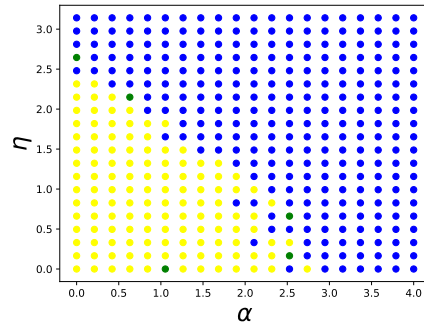
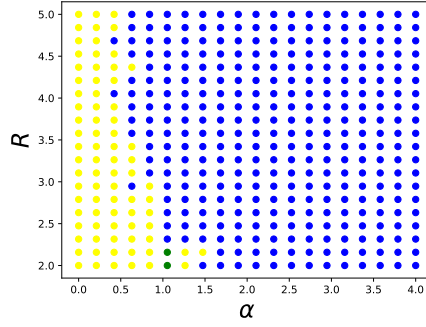
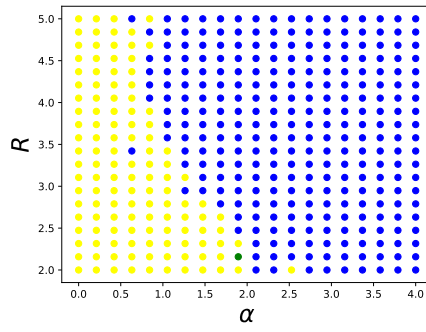


Figure 3.3: Phase plots for α and R . Blue points: only defectors remain. Yellow points: only cooperators remain. For the green points not enough iterations were given.

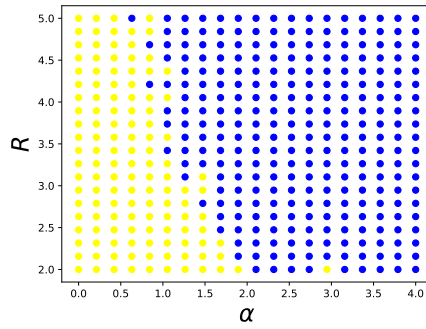
$$\eta = \frac{\pi}{2}$$



$$\eta = \frac{\pi}{4}$$



$$\eta = \frac{\pi}{8}$$



$$\eta = 0$$

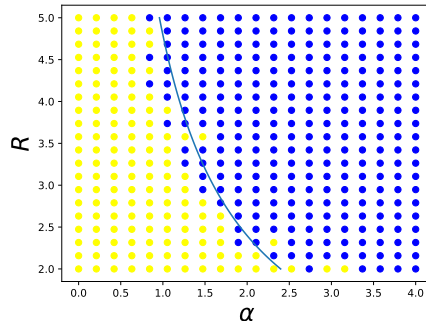


Figure 3.4: Phase in r α space. Blue points: only defectors remain. Yellow points: only cooperators remain. For the green points not enough iterations were given. The curve from figure 3.5 has been placed on the $\eta = 0$ phase plot.

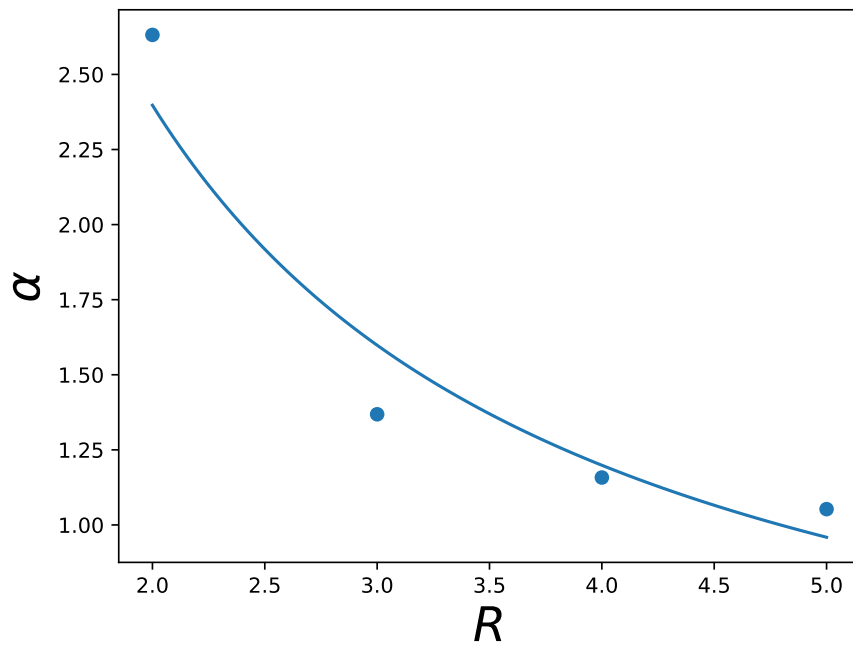


Figure 3.5: The critical values of α at $\eta = 0$ taken from figure 3.3. The curve represents equation 3.8 fitted to the points.

Chapter 4

Two species Vicsek model combined with spring force

In this work, I present a model that combines a weighted Vicsek framework with spring-like interactions. By allowing flexibility in both the alignment weights and spring stiffnesses, the model supports a wide range of interaction strategies. I focus on a special case that resembles the two-species Vicsek model introduced in [6]. I show that this system can rise to rotating clusters with concentric orbital structures. These clusters are analyzed and characterized in detail.

4.1 Introduction

4.1.1 Weighed Vicsek model

In the regular Vicsek model, every neighbor influences a particle equally. However, in reality, some neighbors may affect an individual more than others. This may be because they are family members or because they trust some individuals more than others. There may also be neighbors whom an individual tries to avoid. This could be because they are predators. There might also be neighbours that have no influence at all.

To describe such general interactions, I propose modifying the orientation update rule in the Vicsek model as follows:

$$\theta_j(t+1) = \langle \theta_j(t) \rangle + \Delta\theta \quad (4.1)$$

Here again $\Delta\theta$ is a noise term drawn from a uniform distribution over $[-\eta, \eta]$. The term $\langle \theta_j(t) \rangle$ represents a weighted average of orientations, defined as:

$$\langle \theta_j(t) \rangle = \tan^{-1} \left(\frac{\sin(\theta_j(t)) + \sum_{n \in \Gamma_j(t)} s_{jn} \sin(\theta_n(t))}{\cos(\theta_j(t)) + \sum_{n \in \Gamma_j(t)} s_{jn} \cos(\theta_n(t))} \right) \quad (4.2)$$

Here s_{jn} is a weight that characterizes the influence of particle n on particle j . If $s_{jn} > 0$, j will tend to move in the same direction as n when n is a

neighbor of j . And if $s_{jn} < 0$, j will tend to move in the opposite direction of n when they are neighbors. If $s_{jn} = 0$, n will never directly influence j .

In the regular Vicsek model $s_{jn} = 1$ for every j and n . Defectors from the previous chapter almost behave as if $s_{jn} = 0$ for all n .

The two-species Vicsek model from [6] contains two types. Particles of the same type tend to move in the same direction. While particles of different types tend to move in opposing directions. It was shown that the model could give rise to bands, where each band contains one type [6]. The two-species Vicsek model is a special case of the weighted Vicsek model, where $s_{jn} = 1$ if j and n are of the same type. And $s_{jn} = -1$ if they are of different types.

Let s_j be the vector of all weights s_{jn} for a given j . One can interpret s_j as the strategy of particle j . The weighted Vicsek model allows for many possible strategies, though in this formulation, these strategies are static. Future studies could consider dynamic strategies or models involving birth and death processes.

4.1.2 Vicsek model in terms of forces

To incorporate additional forces into the Vicsek model, it is useful to reinterpret it in terms of force-based motion. Microorganisms often operate in a low Reynolds number regime, where viscous drag dominates and the drag force is linear. The equation of motion in such cases is:

$$m \frac{d\vec{v}}{dt} = -b\vec{v} + \vec{F} \quad (4.3)$$

Here, b is the drag coefficient. F Represents the other forces. The steady-state solution for this equation is:

$$\vec{v} = \frac{\vec{F}}{b} \quad (4.4)$$

This is known as the terminal velocity. Assuming that the terminal velocity is reached instantly (which holds for small m and large b), and choosing $b = 1$, the motion simplifies to:

$$\frac{d\vec{r}}{dt} = \vec{F} \quad (4.5)$$

To get a Vicsek-like model in 2D, one can write:

$$\frac{d\vec{r}_j}{dt} = v_0 \hat{n}(\langle \theta_j \rangle) \quad (4.6)$$

where θ_j is angle of $\frac{d\vec{r}_j}{dt}$. Here, the force is the self-propulsion. Note, this model does not contain torque.

Now that we have a force-based description of the Vicsek model, we may introduce other forces, such as spring forces. Spring models are commonly used to describe solids. Bacteria often attach to other bacteria [22]. One may model the force of the attachment in terms of springs.

Another reason for using spring forces is to incorporate collision-avoidance and attraction, as stated in the main introduction. The spring force between particles j and n is given as:

$$\vec{F}_{jn} = k_{jn}(\vec{r}_n - \vec{r}_j) \frac{||\vec{r}_n - \vec{r}_j|| - l}{||\vec{r}_n - \vec{r}_j||} \quad (4.7)$$

Here k_{nj} is the spring stiffness and l is the equilibrium displacement. For a reciprocal system $k_{jn} = k_{nj}$. It can be interesting to study cases where this is not true. Bacteria will only attach when they are close enough. This will be included in the model. For the sake of simplicity, the spring interaction distance will be equal to the orientation interaction distance. The total spring force acting on particle j then becomes:

$$\vec{F}_j = \sum_{n \in \Gamma_j(t)} k_{jn}(\vec{r}_n(t) - \vec{r}_j(t)) \frac{||\vec{r}_n(t) - \vec{r}_j(t)|| - l}{||\vec{r}_n(t) - \vec{r}_j(t)||} \quad (4.8)$$

Recall that $\Gamma_j(t)$ refers to the particles within distance R of j . One may now add this term to equation 4.9, and get:

$$\frac{d\vec{r}_j}{dt} = v_0 \hat{n}(\langle \theta_j \rangle) + \vec{F}_j \quad (4.9)$$

We now have a model with strategies that consist of two parts, the Vicsek weights s_{jn} and the spring stiffnesses k_{jn} . In the next section, a numerical representation of this model with noise will be given.

4.2 Numerical representation

The position gets updated as:

$$\vec{r}_j(t+1) = \vec{r}_j + \vec{V}_j \quad (4.10)$$

Here, $\vec{V}_j$ is the velocity. The orientation update is:

$$\theta_j(t+1) = \text{Arg}(\vec{V}_j) + \Delta\theta \quad (4.11)$$

Here, Arg refers to the angle. $\Delta\theta$ Is again a random number from a uniform distribution over $[-\eta, \eta]$. This noise term mimics the stochasticity in the standard Vicsek model. The velocity $\vec{V}_j$ is given as:

$$\vec{V}_j = v_0 \hat{n}(\langle \theta_j(t) \rangle) + \vec{F}_j \quad (4.12)$$

Here $\hat{n}$ is once again a unit vector. $\langle \theta_j(t) \rangle$ Is the weighted Vicsek part from Equation 4.2. And $\vec{F}_j$ is the spring force from Equation 4.8.

Now that the numerical representation has been explained, a special case of this model will be explored.

4.3 Two species case

In the two-species case, there are two types: blue and red. If j and n are of the same type, then $s_{jn} = 1$. Likewise, if they are of different types, $s_{jn} = -1$. All the spring stiffnesses are the same, so $k_{jn} = k$ for every j and n .

To do simulations, every particle has initially been randomly placed on a $L * L$ square, with random initial orientations. Periodic boundary conditions have been used. If a parameter is not specified, it will be given in table 4.1. See [28] for code and [1] for animations.

v_0	η	R	L	ρ	k	l
0.1	0	5	31.6	0.5	0.01	2.5

Table 4.1: If I have not specified the value of a parameter, its value will be given in this table. ρ Is the density.

To build intuition, the dynamics when only one species (e.g., red) is present are examined. Figures 4.1 and 4.2 show the result.

In the beginning, the particles move in clusters due to the spring forces. Due to the limited range of the spring forces, these clusters have finite sizes. The clusters eventually merge and form an unstable structure as seen in Figure 4.2. Here we see that the particles tend to either point into the center or away from the center. When the particles get close enough, the spring force pushes them outward. When the particles get far enough apart the spring force pulls them inward.

Now, simulations where half of the particles are red and half of the particles are blue will be examined. Beware that simulations can for some parameters produce results where there are no stable clusters. There are also choices for parameters where there are no clusters at all. I will only focus on cases with stable clusters.

Blue particles should form moving clusters. If a moving cluster of red particles meets a moving cluster of blue particles, the spring force should make them merge together. While the self-propulsion would oppose the merging. Figure 4.3 shows quiver plots resulting from a system where half of the particles are red. Here, one can see that the clusters consist of a red part and a blue part. They rotate since the self-propulsion causes the red and blue parts to move in opposing directions. Looking at the right column, one can see that the red particles in the middle tend to point in the same direction. While in the outer part of the cluster, the red particles tend to point along a curve resembling a circular arc. The reason for this difference could be that the spring force tends to cancel itself out in the middle since there are approximately an equal number of particles on each side. This causes the self-propulsion to be the dominating force. For a particle in the outer part of the cluster, there are more particles on one side than the other. Therefore, the spring forces cause a curved trajectory.

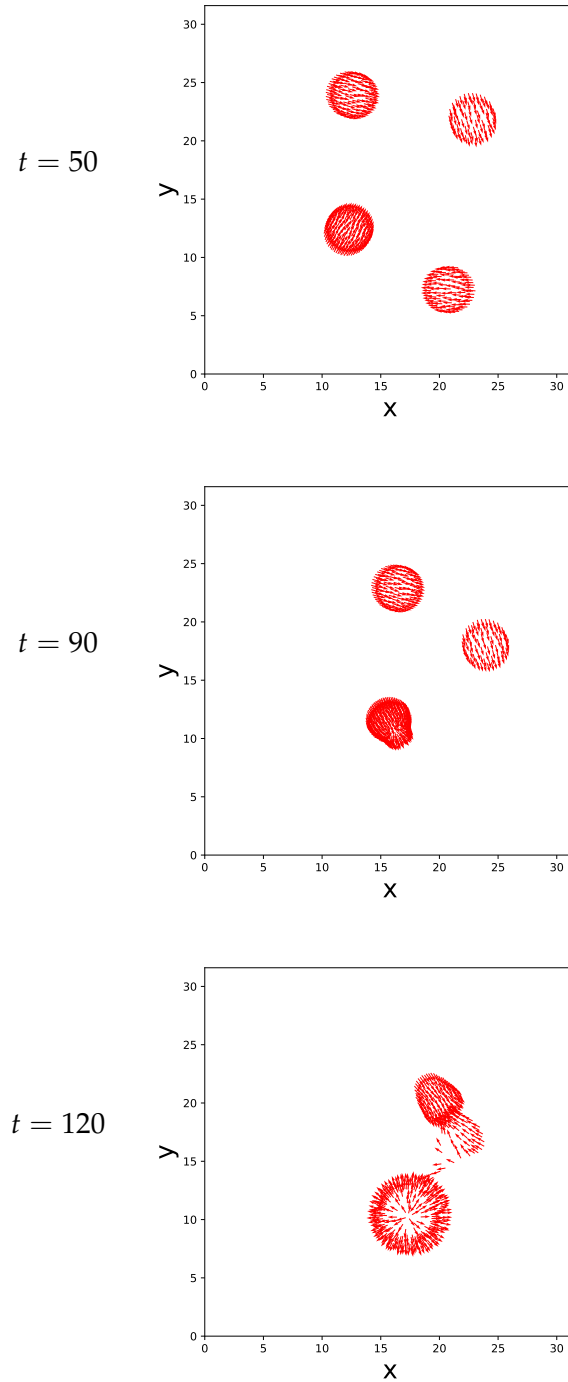


Figure 4.1: Clusters resulting from a system with only red particles, shown at different time steps.

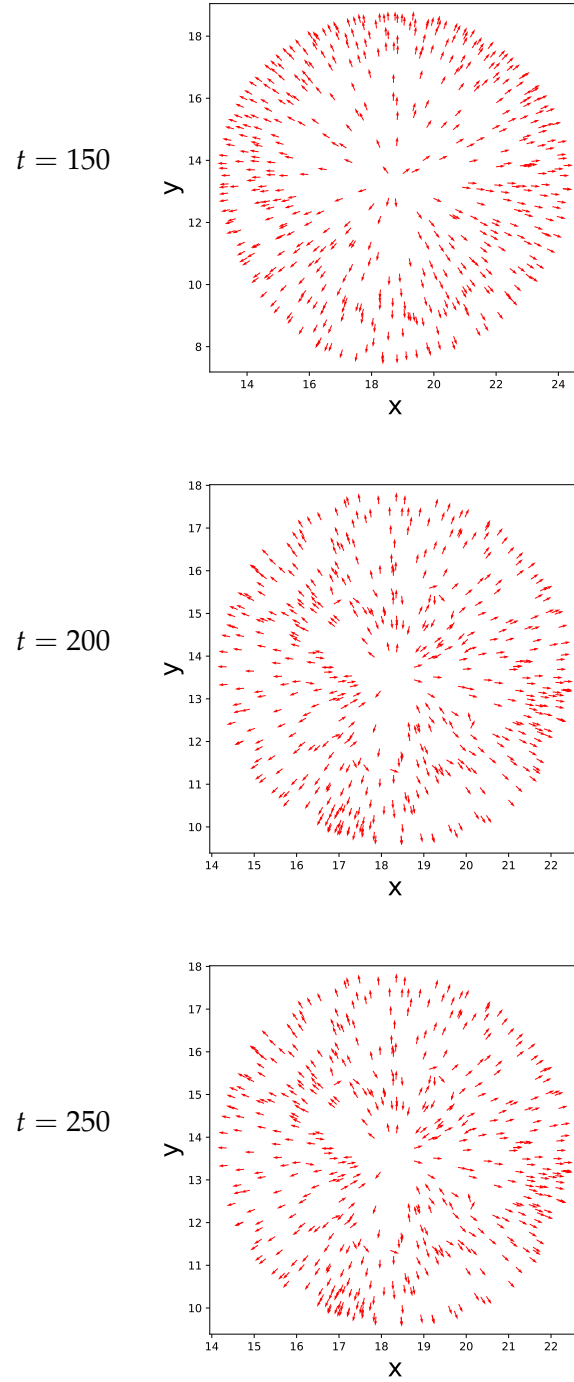
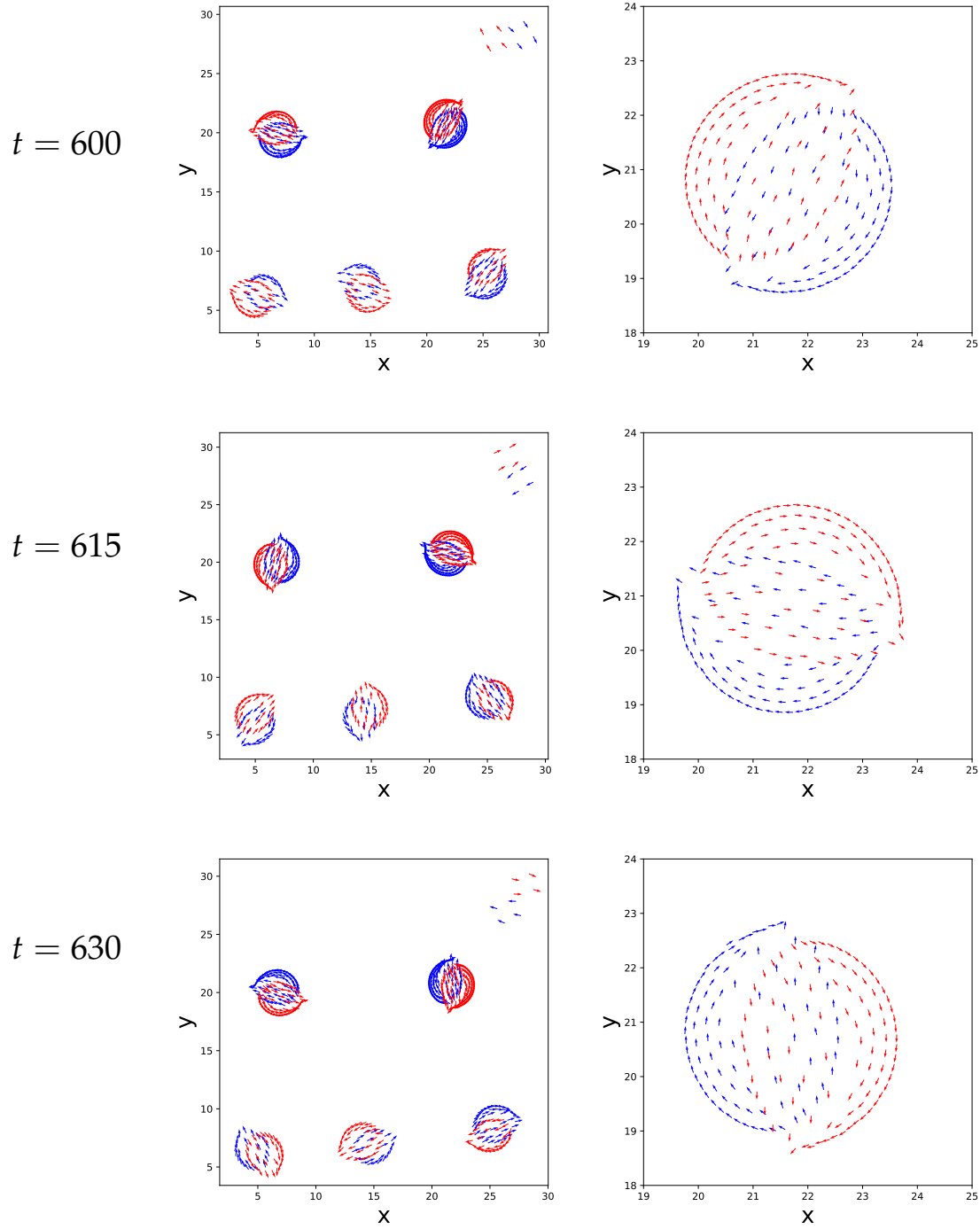


Figure 4.2: Plots showing the result after the clusters in a system with only red particles have merged.

Figure 4.3: A mixture of red and blue particles results in rotating clusters. The plots show results from simulating a system with the parameters given in Table 4.1. In the second column, the large cluster in the upper right has been zoomed in on.



The motion of one of the particles is shown in Figure 4.4. The trajectory

looks like a circular coil. This indicates that the motion consists of two parts. One part comes from the rotation of the cluster. And the other part is an orbit that is stationary with respect to the cluster. The x and y plots indicate two frequencies. They would correspond to the two kinds of motion.

In order to better see the motion, it would be helpful to remove the rotation from the cluster. One can remove the rotation from the cluster, by finding a point $\vec{r}_s$ that is stationary relative to the cluster. One also needs the center of rotation $\vec{r}_{cr}$. To remove the rotation one needs to calculate ϕ , which is the angle of $\vec{r}_s - \vec{r}_{cr}$. One then needs to rotate the cluster by $-\phi$. A transformation that removes the rotation and centers the cluster at the origin is:

$$\vec{r}_j(t) \rightarrow \tilde{R}(-\phi(t))(\vec{r}_j(t) - \vec{r}_{cr}) \quad (4.13)$$

Here, $\tilde{R}$ is the rotation matrix. The transformation for the orientation becomes:

$$\theta_j(t) \rightarrow \theta_j(t) - \phi(t) \quad (4.14)$$

I have assumed that the rotation center is the cluster center. The cluster center is given as:

$$\vec{r}_c(t) = \frac{\sum_{j \in c} \vec{r}_j(t)}{|c|} \quad (4.15)$$

Here, c refers to the particles in the cluster. I have used the blue center as $\vec{r}_s$. The blue center is defined as:

$$\vec{r}_B(t) = \frac{\sum_{j \in B} \vec{r}_j(t)}{|B|} \quad (4.16)$$

Here, B refers to the set of blue particles in the cluster. To make it easier to analyze, I have also rotated the cluster such that the blue center lies on the x axis.

Figure 4.5 shows the result after removing rotation from the cluster in Figure 4.4. There are concentric orbits. The orbits seem to slightly deviate from circular. The x plot seems almost trigonometric.

As previously mentioned, the spring forces cancel each other out where the blue part and the red part intersect. This might explain the orbital motion. In the diagrams shown in Figure 4.6, the blue particle is first in the intersection region and then outside. When it is in the intersection region, it moves since the spring forces don't act against the self-propulsion. When it leaves the intersection region, one can imagine that it enters a chain of particles. It pushes on this chain. This causes the particle at the opposite end of the chain to get pushed into the intersection region. This causes the cycle to repeat.

Now that the behavior has been seen for the parameters given in the table in 4.1, the parameters v_0 and l will be varied. Then how the different properties of the clusters depend on these parameters will be studied.

Ten simulations were performed for ten values of v_0 evenly spaced over the interval $[0.01, 0.3]$. Figure 4.7 shows results for three representative values of v_0 . For $v_0 = 0.01$ the clusters do not consist of a red and a

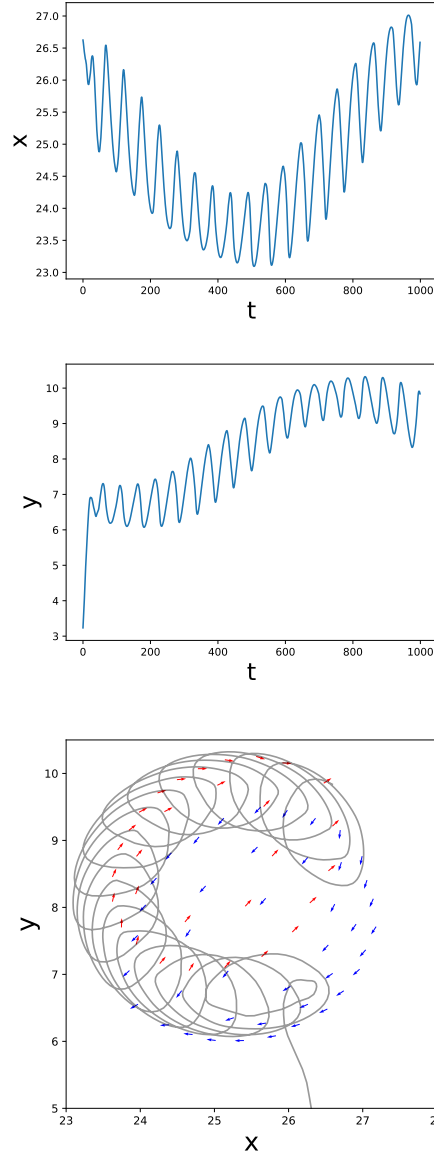


Figure 4.4: These plots show the movement of one of the particles from the simulation corresponding to figure 4.3. The last plot shows part of the trajectory, plotted together with a quiver at iteration 600. The motion seems to consist of two parts: the rotation of the cluster itself and an orbital motion that remains stationary relative to the cluster.

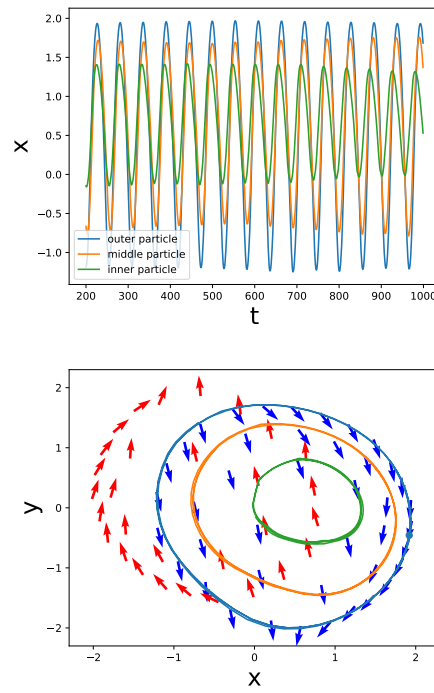


Figure 4.5: Results after removing the global rotation from the cluster shown in Figure 4.4. The bottom panel displays a quiver plot at iteration 1000, overlaid with the trajectories of three particles from $t = 850$ to $t = 999$. The top panel shows the corresponding x -positions of these particles over time.

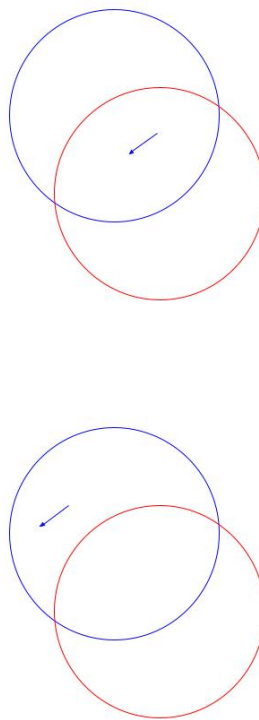


Figure 4.6: Diagram for explaining the motion of the particles relative to the cluster. The blue circle represents the blue cluster, while the red circle represents the red cluster. A blue particle starts off in the intersection between the clusters, where the effect of the spring forces is small. It then goes to a region where the effect of the spring forces is large.

blue part. Instead, the red and blue particles are evenly mixed. The self-propulsion is too weak to separate the clusters. The red and blue particles, do however, anti-align. Based on an animation, these clusters do not seem to rotate. The reason for this is that there are no separate red and blue parts. For the other plots, one can see that the separation between the blue and red parts becomes large with v_0 . The reason for this might be that the spring force requires a larger deviation from the equilibrium length to balance the self-propulsion. For $v_0 = 0.3$, the difference in the amount of blue and red in each cluster tends to be larger than the other v_0 . The reason for this might be that particles can more easily escape regions where cluster formation happens.

Ten values of l in the interval $[0.6, 3]$ have been used. The result for 3 values can be seen in Figure 4.8. Here, one can see that small l create small clusters. For $l = 3$, not all orientations point along a circular arc. This might indicate that clusters are close to being unstable.

4.3.1 Measuring cluster properties

Now that quivers for the different l and v_0 have been shown, different properties of the clusters will be examined, such as their separation distance, cluster rotation rate, and orbital period.

To analyze the clusters, one first needs to identify which particle belongs to which cluster. This can be done manually by drawing boxes around them, or by an algorithm. I have used the k-means clustering algorithm. The goal of the algorithm is to minimize the following quantity:

$$S = \sum_c \frac{\sum_{n \in c} ||r_n - r_c||^2}{|c|} \quad (4.17)$$

Here, c refers to a cluster. This quantity represents the sum of all the cluster variances. The k-means clustering algorithm takes the number of clusters N as an input. In the beginning, N Voronoi cells are made from N random points. The average position in each cell is used to create N new Voronoi cells. Then the process repeats until S is sufficiently small. I have used the Python library SciPy[32] to perform k-means clustering. The number of clusters I got for different v_0 is given in Table 4.2. And the number of clusters I got for different l are given in Table 4.3.

v_0	0.01	0.042	0.074	0.11	0.14	0.17	0.20	0.24	0.27	0.3
Number of clusters	6	4	7	6	4	5	5	4	4	4

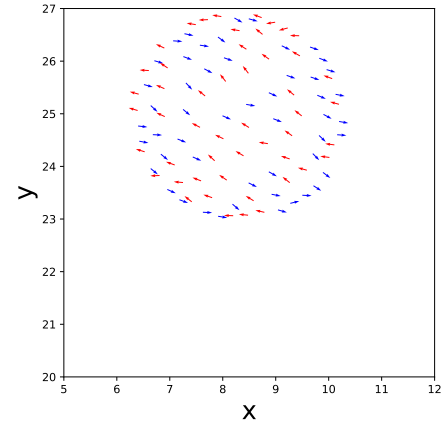
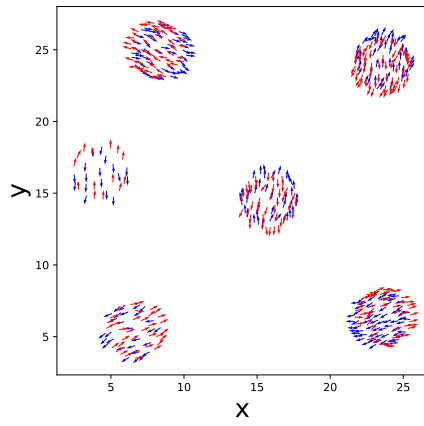
Table 4.2: Number of cluster for different v_0 . Keep in mind that the v_0 have been rounded.

To quantify the separation between the blue and red part, one can measure the distance between the blue and red center. The blue center is defined in Equation 4.16. The red center is similarly defined as:

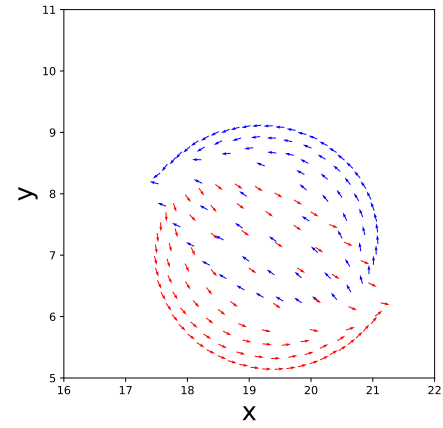
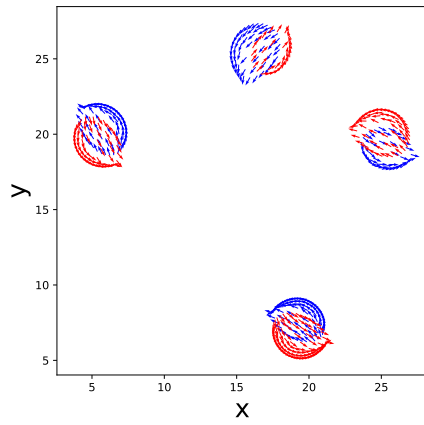
$$\vec{r}_R(t) = \frac{\sum_{j \in R} \vec{r}_j(t)}{|R|} \quad (4.18)$$

Figure 4.7: Result after 1000 iterations with different v_0 . The values for v_0 have been rounded. In the right column, one of the clusters has been zoomed in on.

$$v_0 = 0.01$$



$$v_0 = 0.14$$



$$v_0 = 0.3$$

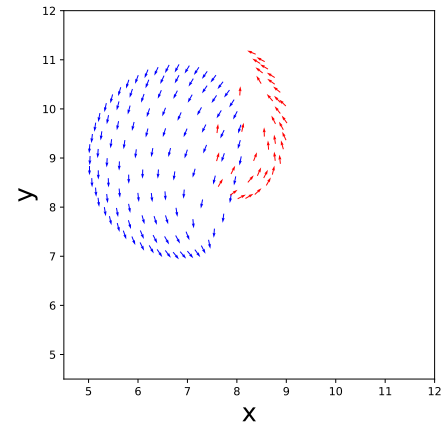
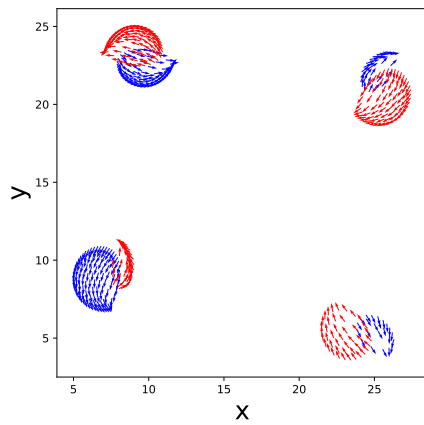
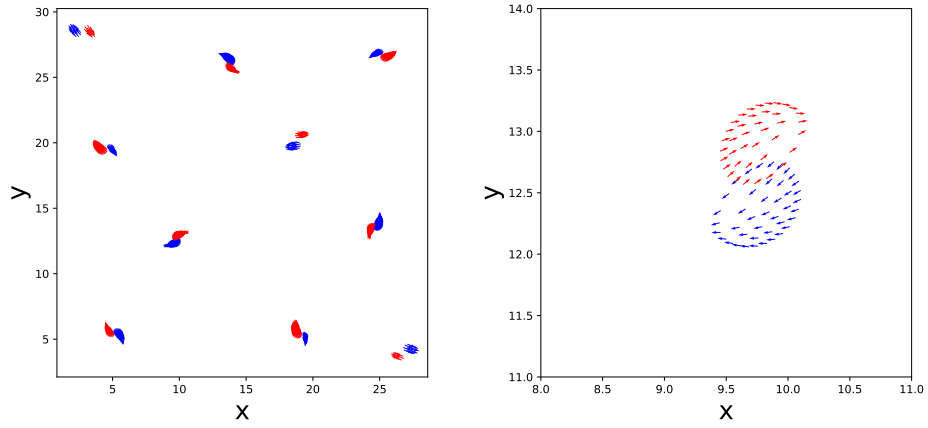
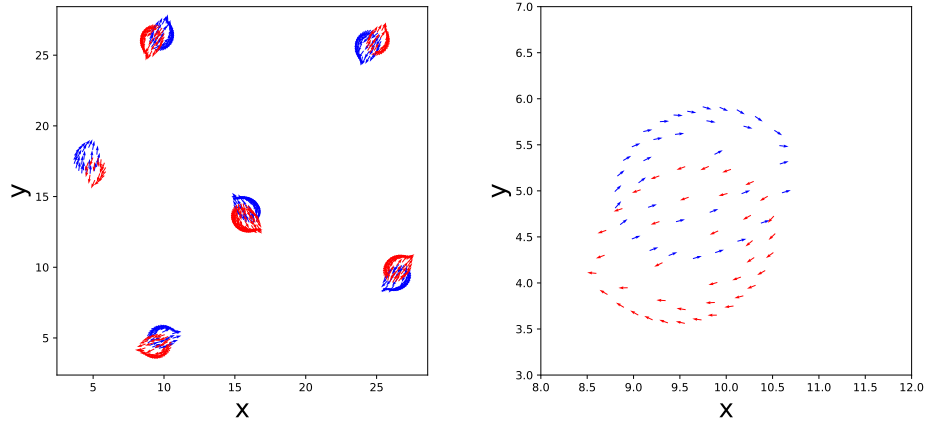


Figure 4.8: Result after 1000 iterations with different l . The values for l have been rounded. One of the clusters has been zoomed in on in the right column.

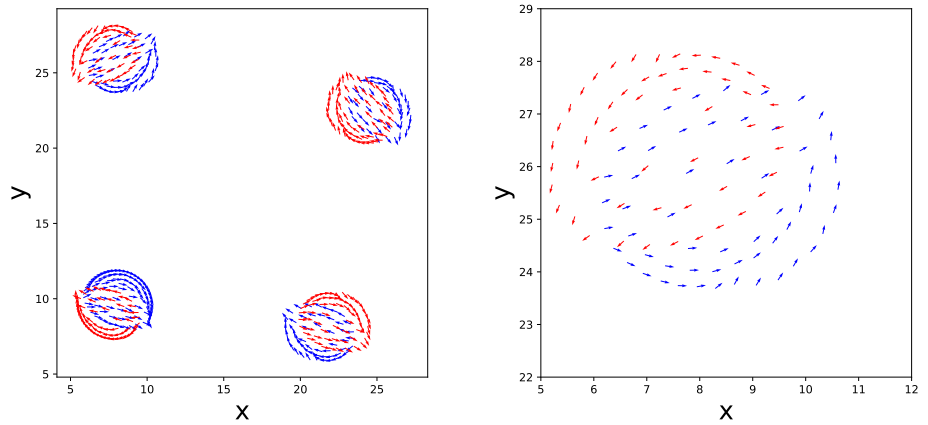
$$l = 0.6$$



$$v_0 = 1.4$$



$$l = 3$$



l	0.6	0.87	1.33	1.4	1.7	1.9	2.2	2.5	2.7	3
Number of clusters	10	8	9	6	7	5	7	6	4	4

Table 4.3: Number of clusters for different l . Keep in mind that the l has been rounded.

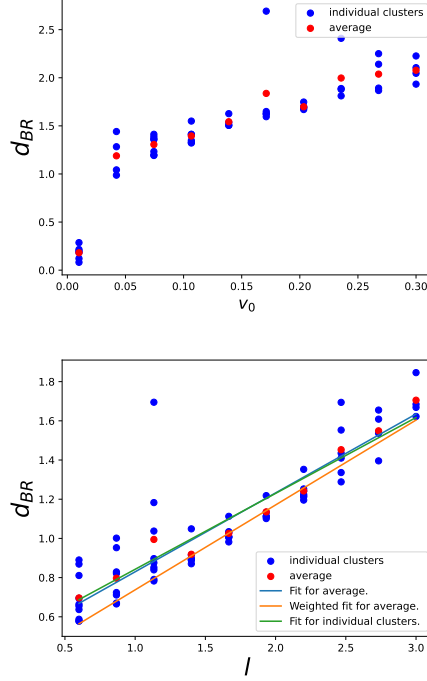


Figure 4.9: The distance between the red center and blue center plotted for l and v_0 . The linear relationship between l and d_{BR} gets tested.

Here, R refers to the set of red particles in the cluster. The distance between the blue and red centers is defined as:

$$d_{BR} = ||\vec{r}_B - \vec{r}_R|| \quad (4.19)$$

I have taken a time average of d_{BR} from $t = 499$ to $t = 999$. The result can be seen in Figure 4.9. For each choice of v_0 and l I have also calculated the average over all clusters.

In order to measure the cluster rotation rate and the orbital period, I have used the discrete Fourier transform. It is defined as:

$$F\{r(t)\}(\omega) = \sum_{-\frac{T-1}{2}}^{\frac{T-1}{2}} r(t) e^{-i\frac{\omega}{T}t} \quad (4.20)$$

The number of points is T . r is the position in terms of complex numbers. The angular velocity is ω . It can take on T values in the range $[-2\pi\frac{T-1}{2}, 2\pi\frac{T-1}{2}]$. To find the cluster rotation rate and the orbital period

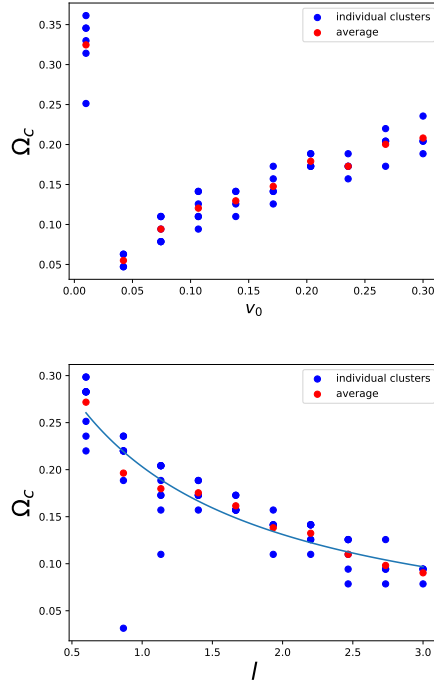


Figure 4.10: Plots showing the cluster rotation rate for different v_0 and l . In the l plot, the curve from Equation 4.29 is included.

one finds the ω that maximizes the following function.

$$A(\omega) = \frac{\sum_{j=0}^N |F\{r_j(t) - \bar{r}_j\}(\omega)|^2}{N} \quad (4.21)$$

Here $\bar{r}_j$ is the time average of r_j . This function takes the average of $|F\{r_j(t) - \bar{r}_j\}(\omega)|^2$ over N different points.

To find the cluster rotation rate for each cluster, I have evaluated A over the blue and red centers. Then the ω that maximizes A has been found. The cluster's rotation rate has been identified as $|\omega|$. Iterations from $t = 600$ to $t = 999$ have been used for this computation. Figure 4.10 shows the cluster rotation rate for each cluster as well as the averages for each simulation.

I have assumed that the orbital period for each particle in a cluster is the same. To compute it for a cluster, the rotation has first been removed using the method described in the previous subsection. Then A has been evaluated over the cluster. After that, the ω that maximizes A has been identified. Then the orbital period has been calculated as:

$$T = \frac{2\pi}{|\omega|} \quad (4.22)$$

Iterations from $t = 600$ to $t = 999$ have been used. The result can be seen in Figure 4.11. The averages of these orbital periods are also included here. Note that $v_0 = 0.01$ has not been included since it did not seem to rotate.

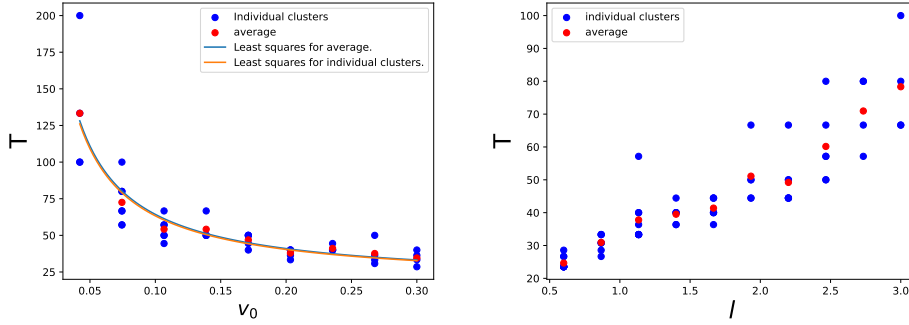


Figure 4.11: Plots of the orbital period for l and v_0 . In the v_0 plot the curve from Equation 4.32 has been fitted to the points.

The distances between the red and blue centers have been measured. The orbital period and cluster rotation rates have been measured using the Fourier transform.

4.3.2 Interpretation of the measurements and theory for the particle movement.

In this subsection, the results from the previous subsection will be discussed. Theories for how the measured quantities depend on the parameters will be given. A theory for how a particle moves inside a cluster will also be given.

In Figure 4.9, one can see that d_{BR} increases with v_0 . For large v_0 , the deviation from the equilibrium length l needs to be large in order for the spring force to outbalance the self-propulsion. This may explain this behavior. d_{BR} seems to approach a value that is a bit lower than l . Recall from Table 4.1 that $l = 2.5$. For large v_0 , there is more variation in d_{BR} . In Figure 4.7, it was shown that for large v_0 , the difference between the number of blue particles and red particles was large. This may explain why there is a lot of variation in d_{BR} for large v_0 .

For the l plot there are outlier clusters for small l . There are a lot of clusters for small l , this may explain the outliers. The following relationship between l and d_{BR} seems to hold true:

$$d_{BR} = \alpha_0 l + \beta_0 \quad (4.23)$$

To test this, three lines have been fitted to the data. One line comes from least squares applied to all the clusters. Another line comes from applying least squares to the averages. And the last line comes from using weighted least squares on the averages. The weights are given as:

$$w = \frac{1}{var(d_{BR})} \quad (4.24)$$

The parameters α_0 and β_0 are given in Table 4.4.

	α_0	β_0
Weighted least squares on average.	0.433	0.304
Regular least squares on average.	0.403	0.427
Least squares on all clusters.	0.387	0.455

Table 4.4: Slope α_0 and intercept β_0 for the linear fittings in Figure 4.9.

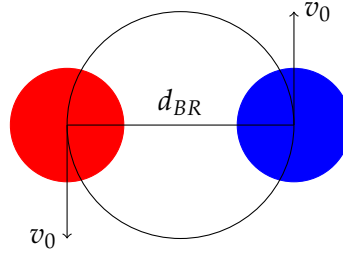


Figure 4.12: Illustrating the situation when the blue and red centers lie on the circle with radius r_s .

The lines for the average and for the individual clusters look almost the same. They seem to fit the data better than the weighted least squares line. The linear relationship indicates that d_{BR} is proportional to the distance between the particles.

I will now attempt to give a theory for the cluster rotation rates. One may imagine that the blue and red parts move along a circular path with velocity v_0 . Let r_s be the radius of this circle. The cluster rotation rate would then be the same as the angular velocity around this circle. The cluster rotation rate will therefore be given as:

$$\Omega_c = \frac{v_0}{r_s} \quad (4.25)$$

r_s Should be proportional to the separation between the red and blue parts. Therefore, r_s should be proportional to d_{BR} , which would lead to the following relation:

$$\Omega_c = \lambda \frac{v_0}{d_{BR}} \quad (4.26)$$

If the blue and red centers lie on the circle with radius r_s , as illustrated in Figure 4.12, the following should be true:

$$r_s = \frac{d_{BR}}{2} \quad (4.27)$$

This would lead to:

$$\lambda = 2 \quad (4.28)$$

The proportionality between $\frac{v_0}{d_{BR}}$ and Ω_c has been tested using three methods. One is by plotting $\frac{v_0}{d_{BR}}$ against Ω_c for the different v_0 . And then using least squares to make a linear fit. $v_0 = 0.01$ Has been dropped from the linear fit. The second method is doing the same for the different l . The $\frac{v_0}{d_{BR}}$ plots can be seen in Figure 4.13.

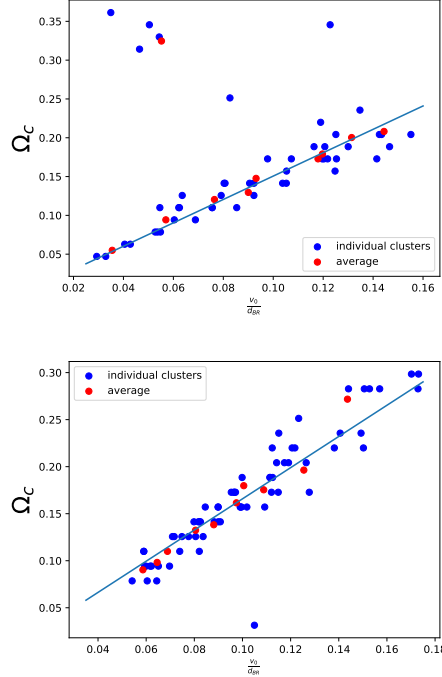


Figure 4.13: Plots showing proportionality between $\frac{v_0}{d_{BR}}$ and Ω_c . The top plot is for different v_0 and the bottom plot is for different l .

α_1	β_1
2.71	2.22

Table 4.5: Parameters for Equation 4.29, which describes the relationship between the cluster rotation rate and the parameter l .

The last method is by fitting a curve to the plot of Ω_c against l in Figure 4.10. Recall that $d_{BR} = \alpha_0 l + \beta_0$. Therefore, one should be able to fit the following curve to the plot with Ω_c against l :

$$\Omega_c = \frac{1}{\alpha_1 l + \beta_1} \quad (4.29)$$

The parameters can be seen in Table 4.5.

The following equations describe the relationship between the parameters from equations 4.23 and 4.29.

$$\alpha_1 = \frac{1}{\lambda v_0} \alpha_0 \quad (4.30)$$

$$\beta_1 = \frac{1}{\lambda v_0} \beta_0 \quad (4.31)$$

One can calculate λ from these equations. Calculating it as an average gives:

$$\lambda = \frac{\frac{\alpha_0}{v_0 \alpha_1} + \frac{\beta_0}{v_0 \beta_1}}{2}$$

	λ
Fitting curve to $\frac{v_0}{d_{BR}}$ plot for different v_0 .	1.51
Fitting curve to $\frac{v_0}{d_{BR}}$ plot for different l .	1.66
Fitting curve to l plot	1.56

Table 4.6: Estimates for the proportionality coefficient between $\frac{v_0}{d_{BR}}$ and Ω_c .

Using this equation, I have calculated λ from the parameters corresponding to the linear fit for all clusters in Figure 4.9. The estimates for λ coming from $\frac{v_0}{d_{BR}}$ plots and l plot can be seen in table 4.6.

Figure 4.13 shows that the linear relationship between $\frac{v_0}{d_{BR}}$ seems to hold. However, there are many outliers. The plot for different v_0 gives a lower λ than the plot for different l . The fitted curve in the l plot in Figure 4.9 seems to fit well. This indicates a linear relationship between $\frac{v_0}{d_{BR}}$ and Ω_c , as well as between l and d_{BR} . The estimates for λ in Table 4.6 are close. The average is 1.58. Recall that if the red and blue centers were on the circle with radius r_s , then $\lambda = 2$. The estimated value of λ is less than 2. This implies that the circle on which the red and blue parts move lies farther out than the red and blue centers.

In Figure 4.11, one can see that the orbital period decreases with increasing v_0 . This makes sense since a higher v_0 would typically imply a higher velocity. One can also see that higher l leads to longer orbital periods. It has already been shown that the clusters were small for low l . This implies that the length of orbit is shorter for low l , which could explain the shorter period. For large l there is more variation for the orbital period. This could imply that the clusters differ more in shape.

I will now attempt to find a theory for how the orbital period depends on v_0 . To do this, the orbital period will be divided into two smaller periods. For the first period, the particles stay close to the center of the cluster. Here, the spring forces tend to get canceled out as previously mentioned. This means that particles will tend to move with velocity γv_0 , where γ is a proportionality constant. Let the distance the particles travel during this period be d . Therefore, this period becomes $\frac{d}{\gamma v_0}$. Let T_∞ be the rest of the orbital period. Therefore, the entire orbital period becomes:

$$T = \frac{d}{\gamma v_0} + T_\infty \quad (4.32)$$

To test this, least squares were used to fit a curve from this equation in Figure 4.11. This was done for both the averages and the individual clusters. The parameters are given in Table 4.7. Both curves look similar and seem to fit the data well.

I will now attempt to give a parametric representation of the movement of the particle in a cluster. As previously mentioned, the movement consists of two parts. The rotation of the cluster and the orbital movement. Therefore, the movement of a blue particle j may be described as:

$$\vec{r}_j = \tilde{R}(\Omega_c(t - t_0))(\rho(\phi, q)\hat{n}(\phi) + \vec{r}_{BO}) + \vec{r}_c \quad (4.33)$$

	$\frac{d}{\gamma}$	T_∞
For individual clusters	4.59	17.46
For averages	4.66	17.66

Table 4.7: Parameters for the equation describing how the orbital period depends on v_0 (see Equation 4.32).

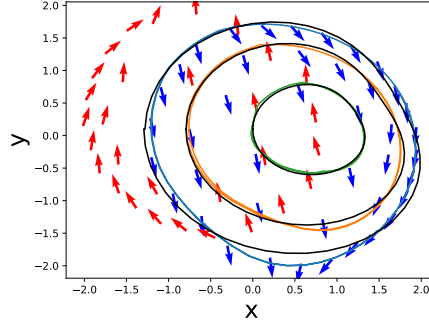


Figure 4.14: Fitting orbits with Gaussian dents to trajectories where the rotation has been removed.

Here $\tilde{R}$ is the rotation matrix, that rotates the vector $\rho(\phi, q)\hat{n}(\phi) + \vec{r}_{BO}$ around the cluster center $\vec{r}_c$ by the angle $\Omega_c(t - t_0)$. t_0 Refers to the phase for this rotation. From the blue orbital center r_{BO} , the motion is described in terms of polar coordinates, where the angle is ϕ and the radius is ρ . $\hat{n}$ Is a unit vector. q Is an integer that specifies the orbit that j lies on. The orbit closest to the orbital center has $q = 0$, while the orbit farthest away has $q = o - 1$. Where o is the total number of orbits.

To find ρ , I have tried a circle with a dent. In this case ρ can be expressed as:

$$\rho(\phi) = \rho_0 D(\phi - \phi_0, w, H) \quad (4.34)$$

Here, ρ_0 is the radius of the circle. D Is a dent that is centered at ϕ_0 , with width w and length H . If $D > 1$ the dent points outward, and if $D < 1$ the dent points inward. I have tried a Gaussian for D . It can be expressed accordingly:

$$D(\phi, w, H) = 1 + He^{-\frac{\phi^2}{2w^2}} \quad (4.35)$$

I have tried to fit this equation to the trajectories in Figure 4.5. For the center of the orbits, I used $r_{BO} = [0.7, 0, 1]$. I used iterations from $t = 900$ to $t = 999$. The fitted curves can be seen in Figure 4.14, and the curve parameters can be seen in Table 4.8.

From Figure 4.14, one can see that the further in an orbit is the better the curve fits. The orbits further in are also more circular. This can be seen from Table 4.8, where both w and $|H|$ get smaller for orbits further in. The reason for inner orbits becoming more circular than outer orbits, could be that outer orbits get closer to the middle of the cluster, where the spring forces will tend to get canceled out.

	ρ_0	ϕ_0	w	H
Outer orbit	1.99	0.432	0.941	-0.442
Middle orbit	1.49	0.483	0.803	-0.369
Inner orbit	0.700	0.493	0.551	-0.172

Table 4.8: Parameters used for fitting curves to orbits.

How different v_0 and l affect the motion has been studied. The orbital period, cluster rotation rate, and the distance between the blue and red centers have been measured for different choices of parameters. The relationship between the distance between the red and blue centers d_{BR} and l , is described by Equation 4.23. The cluster rotation rate has been found to be described by Equation 4.26. The dependence of the orbital period on v_0 has been found to be described by Equation 4.32.

The orbital trajectories have been studied for a single cluster. The orbits seem to be dented circles.

4.4 Conclusion

A Vicsek model augmented with spring forces can give rise to moving clusters. When two distinct particle types (red and blue) are introduced, where particles of the same type tend to align and particles of different types tend to anti-align, red and blue clusters can attach and form a composite cluster, with each type occupying a distinct region. The anti-alignment property, together with self-propulsion, causes the clusters to rotate.

These rotating clusters can have concentric orbital motion, likely caused by the cancellation of spring forces in the central region. I have characterized these structures by analyzing their rotation rate, orbital period, and the spatial separation between the red and blue parts. Theoretical models have been proposed to explain these observed quantities.

There is ongoing research concerning how single cells join together and form a spatial structure. The model in this chapter could potentially be applied to this. One could imagine that the different particle types represent different cell types. This model could therefore help explain how different cell types end up in different regions of a multi cellular structure.

A real system similar to the system presented in this chapter would be more complicated. For one, there would be centrifugal effects, which could cause the red and blue parts to have outward dents. If the clusters were large enough and rotated sufficiently fast, the Coriolis effect could have an impact. It would probably give the orbits more complicated shapes. If the particles are close enough, there could be collective drag, meaning that the drag force a particle experiences when moving alone is different from the drag force it experiences while being in a cluster.

Chapter 5

Chemotaxis model

I present a chemotaxis model involving self-propelled particles that move at a constant speed and interact with both a nutrient concentration and a chemical signal. Simulations with a uniform initial nutrient concentration reveal the emergence of dots, stripe patterns, and moving clusters. When nutrient growth is introduced, the system develops sparse particle spots. I have also tried using a Gaussian for the initial nutrient concentration. This has caused particles to gather at the center of the Gaussian. And then leaving it as the nutrients get consumed.

5.1 Introduction

Until now, the particles in the previous models have updated their orientations based on their neighbors' orientations. In this chapter, a model where particles update their orientations based on concentration gradients will be presented. Many organisms respond to chemicals in their environment.

For instance, many organisms move in response to nutrients. They would typically move from a location that is high in nutrients to a place that is low in nutrients. We may therefore say that they follow the gradient of the nutrient concentration. It is a well-known fact that bacteria often follow a nutrient gradient [17]. Organisms also change the nutrient concentration by consuming the nutrients.

Many organisms secrete chemical signals—substances used to communicate with other organisms. It is often the case that other organisms will move towards a chemical signal. For instance, ants secrete pheromones. When ants travel between locations, they leave behind a pheromone trail that other ants follow. The pheromones evaporate, so if new pheromones are not added by ants using the trail, the trail will disappear [9]. We may describe the attraction towards a chemical signal in terms of movement following a chemical signal gradient.

The study of how organisms move in response to chemicals is called chemotaxis. Usually, the organisms are modeled as a concentration field rather than as individual particles. The Keller Segel model is commonly used for this [23]. It contains a partial differential equation describing the

organism concentration. And one or more partial differential equations describing chemical concentrations. For the case when the organisms only interact with a chemical signal, the Kellers Segel model gives the following organism concentration equation:

$$\frac{\partial b}{\partial t} = \nabla \cdot (D_b(b, c) \nabla b - b \chi(b, c) \nabla c) + f(b, c) \quad (5.1)$$

Here, b is the organism concentration. c Is the concentration of a chemical signal. The first term describes the current density. The density of the diffusion current is $-D_b(b, c) \nabla b$. The density of the current moving in the direction of the chemical signal gradient is $b \chi(b, c) \nabla c$. The velocity from this movement is $\chi(b, c) \nabla c$. Here χ is the chemotactic sensitivity, which determines how much the organisms are affected by the chemical signal gradient. The birth and death rate is given by $f(b, c)$. The equation describing the chemical signal is:

$$\frac{\partial c}{\partial t} = D_c \nabla^2 c + g(b, c) \quad (5.2)$$

Here, the first term is the diffusion term. The second term describes the destruction and creation of the chemical signal. The organism equation and the chemical signal equation are a set of coupled reaction-diffusion equations. Reaction-diffusion equations can form Turing patterns. Meaning that the concentrations can form stripes and dots[19].

The model I have used is different from the Keller-Segel model in that organisms are represented with individual particles and not concentration fields. The model is inspired by the model from [15]. In this model, the particles move in 2D with constant absolute velocity v_0 . Therefore, the position of particle j is described by the following equation:

$$\dot{\vec{r}}_j = v_0 \vec{p}_j \quad (5.3)$$

Here $\vec{p}_j$ is the orientation vector. It has a magnitude of one and describes the direction of travel. The nutrient gradient and chemical signal gradient create torques. It is assumed that the rotational velocity is proportional to the total torque. This assumption works when the drag coefficient is high and the moment of inertia is low. Under this assumption, the equation describing the angle of the orientation vector becomes:

$$\dot{\theta}_j = \alpha \vec{p}_j \times \nabla n + \beta \vec{p}_j \times \nabla c \quad (5.4)$$

Here, n is the nutrient concentration and c is the chemical signal concentration. α And β are parameters that determine how much the two gradients affect the orientation. The combinations of these parameters can be viewed as a strategy. In [15] they tried evolving these parameters using machine learning. Each particle had the goal of getting to the maximum nutrient concentration.

The equation describing the nutrients was:

$$\frac{\partial n}{\partial t} = D_n \nabla^2 n - k \sum_j n(\vec{r}_j, t) \delta(\vec{r} - \vec{r}_j) \quad (5.5)$$

Here, the first term is the diffusion term, with D_n as the diffusion coefficient. The second term is the consumption coming from each particle, where k is the consumption coefficient. The chemical signal equation they used was:

$$\frac{\partial c}{\partial t} = D_c \nabla^2 c - Ec + a \sum_j \delta(\vec{r} - \vec{r}_j) \quad (5.6)$$

Here again, the first term represents the diffusion with D_c as the diffusion coefficient. The second term represents the decay of the chemical signal. With E as the decay coefficient. The last term represents the secretion of the chemical signal from each particle. The rate at which the secretion happens is a .

The steady-state equation for the chemical signal can be solved exactly for the case when there is one particle moving at constant velocity. The chemical signal equation will now be solved for this scenario. Assume that there is a particle at the origin moving in the x direction with velocity v_0 . It will later be shown how this can be generalized to all directions. Applying the Galilean transform to the time derivative gives:

$$\frac{\partial c}{\partial t} \rightarrow \frac{\partial c}{\partial t} + v_0 \frac{\partial c}{\partial x} \quad (5.7)$$

Therefore, the steady equation becomes:

$$0 = D_c \nabla^2 c - Ec + a \delta(\vec{r}) + v_0 \frac{\partial c}{\partial x} \quad (5.8)$$

The Fourier transform is defined as:

$$\hat{c}(\mathbf{k}) = \frac{1}{2\pi} \int_{-\infty}^{\infty} d^2\mathbf{r} c(\mathbf{r}) e^{-i\mathbf{k}\cdot\mathbf{r}}, \quad c(\mathbf{r}) = \int_{-\infty}^{\infty} d^2\mathbf{k} \hat{c}(\mathbf{k}) e^{i\mathbf{k}\cdot\mathbf{r}}$$

Applying the Fourier transform to equation 5.8 gives:

$$0 = -k^2 D_c \hat{c} - E \hat{c} + \frac{a}{2\pi} + i v_0 k_x \hat{c} \quad (5.10)$$

Rearranging and applying the inverse Fourier transform gives:

$$c(\vec{r}) = \frac{a}{2\pi} \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} \frac{e^{i\vec{k}\cdot\vec{r}}}{D_c(k_x^2 + k_y^2) - i v_0 k_x + E} dk_x dk_y \quad (5.11)$$

The integral will now be done for the case when $v_0 = 0$. It will be generalized afterwards.

$$c(\vec{r}) = \frac{a}{2\pi} \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} \frac{e^{i\vec{k}\cdot\vec{r}}}{D_c(k_x^2 + k_y^2) + E} dk_x dk_y \quad (5.12)$$

Writing the integral in terms of polar coordinates, it becomes:

$$c(r) = \frac{a}{2\pi} \int_0^{\infty} \int_0^{2\pi} \frac{e^{i k r \cos(\theta)}}{D_c k^2 + E} k d\theta dk \quad (5.13)$$

The θ integral is written in terms of the modified Bessel function of the first kind below [10].

$$J_0(kr) = \frac{1}{2\pi} \int_0^{2\pi} e^{ikrcos(\theta)} d\theta. \quad (5.14)$$

Now we may write:

$$c(r) = a \int_0^\infty \frac{J_0(kr)}{D_c k^2 + E} k dk. \quad (5.15)$$

Now, by using the substitution $u = kr$, this integral becomes:

$$\begin{aligned} c(r) &= a \int_0^\infty \frac{J_0(u)}{D_c u^2 + E r^2} u du \\ &= \frac{a}{D_c} \int_0^\infty \frac{J_0(u)}{u^2 + \left(\sqrt{\frac{E}{D_c}} r\right)^2} u du \\ &= \frac{a}{D_c} K_0 \left(\sqrt{\frac{E}{D_c}} r \right), \end{aligned} \quad (5.16)$$

Here, the Hankel transform is applied to the function $\frac{1}{u^2 + \left(\sqrt{\frac{E}{D_c}} r\right)^2}$, resulting in the modified Bessel function of the second kind, K_0 [24].

Now v_0 will be included. To do so k_x in equation 5.11 will be substituted in such a way that the integral resembles the case when $v_0 = 0$. Completing the square gives:

$$k_x^2 - \frac{ivk_x}{D_c} = \left(k_x - \frac{iv_0}{2D_c} \right)^2 + \frac{v_0^2}{4D_c} \quad (5.17)$$

The following substitution will be used:

$$k'_x = k_x - \frac{iv_0}{2D_c} \quad (5.18)$$

One can now write the integral as:

$$c(\vec{r}) = \frac{a}{2\pi D_c} \int_{-\infty}^\infty \int_{-\infty}^\infty \frac{e^{i\vec{k}' \cdot \vec{r}} e^{-\frac{v_0 x}{2D_c}}}{(k'^2_x + k'^2_y) + \frac{v_0^2}{4D_c^2} + \frac{E}{D_c}} dk'_x dk_y \quad (5.19)$$

This integral can be evaluated in the exact same way the integral for $v = 0$ was evaluated. One then gets the following expression:

$$c(r) = \frac{a}{D_c} K_0 \left(\sqrt{\frac{E}{D_c} + \frac{v_0^2}{4D_c^2}} r \right) e^{-\frac{v_0}{2D_c} x} \quad (5.20)$$

To generalize this expression to a velocity in any direction, one can use the fact that $x = r \cos(\theta)$, and get:

$$c(r) = \frac{a}{D_c} K_0 \left(\sqrt{\frac{E}{D_c} + \frac{v_0^2}{4D_c^2}} r \right) e^{-\frac{v_0 r \cos(\theta)}{2D_c}} \quad (5.21)$$

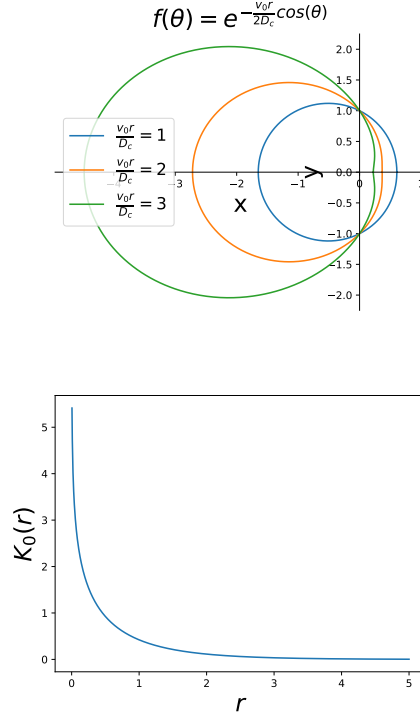


Figure 5.1: The chemical signal in Equation 5.21 is a product of two functions, a modified Bessel function and a polar function. Here, the plots for these two functions are shown.

Plots for $K_0(r)$ and $e^{-\frac{v_0 r \cos(\theta)}{D_c}}$ can be seen in Figure 5.1. $c(r)$ Gets scaled by $\frac{a}{D_c}$. In Figure 5.1, one can see that K_0 decays quickly for r larger than 1. This means that $c(r)$ decays quickly for r larger than $\frac{1}{\sqrt{\frac{E}{D_c} + \frac{v_0^2}{4D_c^2}}}$, so interactions

between particles beyond this range can often be neglected. This is similar to the Vicsek model, where particles only interact when they are within distance R of each other. The polar factor causes radial asymmetry. This can be seen in Figure 5.1. Here, the polar functions become smaller in the front than behind. The amount of rotational asymmetry is determined by $\frac{v_0 r}{D_c}$. In the polar plot, one can see that the difference between the back and front is greater for large $\frac{v_0 r}{D_c}$. For the largest $\frac{v_0 r}{D_c}$, the plot has an inward dent at $\theta = 0$.

The model that I have used differs from the model in [15] in two ways. In nature, organisms reproduce. If the number of individuals in a given species gets too large they start to die. To account for this, I have included a logistic growth term in the nutrient equation. It then becomes:

$$\frac{\partial n}{\partial t} = D_n \nabla^2 n - k \sum_j n(\vec{r}_j, t) \delta(\vec{r} - \vec{r}_j) + \lambda n(1 - Kn) \quad (5.22)$$

Here λ is the growth coefficient. The carrying capacity is $\frac{1}{K}$. If c gets larger than this number, the nutrients start to decay. The second difference is in the orientation. I have assumed that the particles orient themselves

immediately. The orientation vector is defined as a weighted average between the direction of the nutrient gradient and the direction of the chemical signal gradient. The orientation vector is given below.

$$\vec{p}_j = \begin{cases} \frac{\nabla n}{\|\nabla n\|}, & \nabla c = 0, \nabla n \neq 0 \\ \frac{\nabla c}{\|\nabla c\|}, & \nabla n = 0, \nabla c \neq 0 \\ \alpha \frac{\nabla n}{\|\nabla n\|} + (1 - \alpha) \frac{\nabla c}{\|\nabla c\|}, & \nabla n \neq 0, \nabla c \neq 0 \\ 0, & \nabla n = 0, \nabla c = 0 \end{cases} \quad (5.23)$$

Here, there is no β , unlike Equation 5.4. α Determines how much the particles follow the nutrient gradient versus the chemical signal gradient. If $\alpha = 1$, the particles only follow the nutrient gradient. Likewise, if $\alpha = 0$, the particles only follow the chemical signal gradient. α Can be considered a strategy. If one wants to include machine learning into the model, one can use machine learning to change α for the different particles. In the next section, a numerical representation of the model will be given.

5.2 Numerical representation

The particles' positions will be updated using an Euler-based scheme, and the concentrations will be updated using a finite difference method-based scheme. These two methods evolve the system forward one timestep Δt at each iteration. Δt Will not be included in the numerical update equations. However, in the next section, the parameters will be given in terms of Δt . It is important to note that the finite difference method is not stable for every choice of Δx and Δt [5].

I have used a $L * L$ square with periodic boundary conditions. The center has coordinates $[\frac{L}{2}, \frac{L}{2}]$. The spacing is given as:

$$\Delta x = \Delta y = \frac{L}{G} \quad (5.24)$$

Here, G is the number of grid points along one of the axes. The positions need to be discretized in order for the particles to interact with the concentrations. Therefore, the following indices are used:

$$l = \lfloor \frac{x_j}{\Delta x} \rfloor \quad (5.25)$$

$$m = \lfloor \frac{y_j}{\Delta y} \rfloor \quad (5.26)$$

From this, one can give the orientation vector as:

$$\vec{p}_j(t) = \begin{cases} \frac{\nabla n(r_{lm}, t)}{\|\nabla n(r_{lm}, t)\|}, & \nabla c(r_{lm}, t) = 0, \nabla n(r_{lm}, t) \neq 0 \\ \frac{\nabla c(r_{lm}, t)}{\|\nabla c(r_{lm}, t)\|}, & \nabla n(r_{lm}, t) = 0, \nabla c(r_{lm}, t) \neq 0 \\ \alpha \frac{\nabla n(r_{lm}, t)}{\|\nabla n(r_{lm}, t)\|} + (1 - \alpha) \frac{\nabla c(r_{lm}, t)}{\|\nabla c(r_{lm}, t)\|}, & \nabla n(r_{lm}, t) \neq 0, \nabla c(r_{lm}, t) \neq 0 \\ 0, & \nabla n(r_{lm}, t) = 0, \nabla c(r_{lm}, t) = 0 \end{cases} \quad (5.27)$$

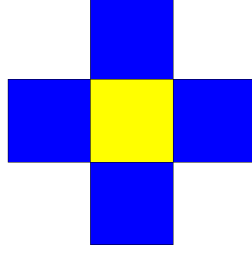


Figure 5.2: Figure illustrating the benefit of central derivative. Here the blue squares have the same value, but the yellow square differs.

Here, the gradients are based on the central derivative.

$$\nabla f = \left[(f_{(l+1)m} - f_{(l-1)m}) \frac{1}{2\Delta x}, (f_{l(m+1)} - f_{l(m-1)}) \frac{1}{2\Delta y} \right] \quad (5.28)$$

The reason for using a central derivative is to avoid direction bias. Consider the gradient at the yellow square in Figure 5.2. Let the yellow square take on the value Y and the blue square take on the value B . And let the x and y indices for the yellow square be l and m respectively. A forward derivative would give the following gradient:

$$\nabla f_{lm} = \left[\frac{f_{(l+1)m} - f_{lm}}{\Delta x}, \frac{f_{l(m+1)} - f_{lm}}{\Delta y} \right] = \left[\frac{B - Y}{\Delta x}, \frac{B - Y}{\Delta y} \right] \quad (5.29)$$

We now see that if $B > Y$, a forward derivative would give a gradient pointing up and right. A backward derivative would give a gradient in the opposite direction. If $B < Y$, the opposite would be true. Central derivative would in this case give 0 as the gradient, and therefore, the direction bias would be avoided.

The position is updated as:

$$\vec{r}_j(t+1) = \vec{r}_j(t) + v_0 \vec{p}_j(t) \quad (5.30)$$

The concentrations are updated accordingly:

$$c(r_{lm}, t+1) = c(r_{lm}, t) + D_c \nabla^2 c(r_{lm}, t) - Ec(r_{lm}, t) + Na \quad (5.31)$$

$$n(r_{lm}, t+1) = n(r_{lm}, t) + D_n \nabla^2 n(r_{lm}, t) + \lambda n(r_{lm}, t)(1 - Kn(r_{lm}, t)) - Nkc(r_{lm}, t) \quad (5.32)$$

∇^2 Is the numerical Laplacian. It is defined as:

$$\nabla^2 f = \frac{f_{(l+1)m} - 2f_{ml} + f_{(l-1)m}}{\Delta x^2} + \frac{f_{l(m+1)} - 2f_{ml} + f_{l(m-1)}}{\Delta y^2} \quad (5.33)$$

N Is the number of particles at that position. Which is the number of particles that satisfy equations 5.25 and 5.26.

5.3 Result

Parameters that are the same in all simulations are given in Table 5.1. The initial positions have been randomly placed on the $L * L$ square. The chemical signal concentration has been initialized as zero everywhere. See the Github repository [26] for code.

5.3.1 Evenly spread initial nutrient concentration

Simulations were conducted for three setups using a constant initial nutrient concentration of 1, with no nutrient regeneration. The parameters for these setups are shown in Tables 5.2, 5.3, and 5.4. The results are seen in figures 5.3, 5.4, and 5.5.

In Figure 5.3, there is a stripe pattern. The particles move along paths where the concentration of the chemical signal is high. The nutrient concentration is relatively high between these paths. Setup 2 differs from Setup 1 in that v_0 is lower. This leads to the spot pattern seen in Figure 5.4. What probably happens is that the particles cannot travel far enough from the center of a cluster to enable connection with another cluster. Recall from Equation 5.21, that the asymmetry was given as $\frac{v_0}{D_c}$. This ratio is two times larger for Setup 1 than for Setup 2. Therefore, the patterns in Setup 2 have higher rotational symmetry than the patterns given by Setup 1. The stripes and dots from Setup 1 and 2 are similar to the pattern formed from other chemotaxis models [23].

Figure 5.5 shows that Setup 3 doesn't form stationary structures. Instead, there are moving clusters. One can see that they are moving since the clusters form tails where the chemical signal is high. Recall from Equation 5.21 that the chemical signal dropped fast for distances larger than $\sqrt{\frac{1}{\frac{E}{D_c} + \frac{v_0^2}{4D_c^2}}}$. For Setups 1 and 2, this number is 0.004 and 0.02, respectively. For setup 3 it is 0.04. This large difference might explain why Setup 3 has a few clusters containing many particles, whereas the other setups do not. The nutrients get consumed fast near the clusters since there are a lot of particles.

Particles within a cluster can be unevenly distributed, causing nutrients to be consumed more rapidly in some regions than in others. This creates a nutrient gradient that drives the movement of the cluster.

Imagine two clusters colliding head-on while moving along the x axis. After the collision, the nutrient concentration becomes depleted along the x -axis, but remains high above and below the x -axis. As a result, two

L	Δt	G	N
31.6	10^{-5}	100	499

Table 5.1: Parameters that are the same for all simulations. G Refers to the grid size. N refers to the number of particles.

v_0	α	D_n	k	D_c	E	a
0.5	0.5	$1000\Delta t$	$1000\Delta t$	$100\Delta t$	$1\Delta t$	$100\Delta t$

Table 5.2: Parameters for Setup 1. These parameters give rise to a stripe pattern.

clusters form: one moving upward and the other moving downward. This splitting behavior can be seen in the plots in Figure 5.5.

Another behavior seen for Setup 3 is the bending of the cluster. The clusters are attracted to their tails, and this causes bending.

Setup 3 gives behavior that looks like flocking. The behavior is similar to the behavior seen in the Vicsek model for small radii.

For the three setups, I have also used regeneration of nutrients. I have used the growth coefficient of $\lambda = 1000\Delta t$. I have used $K = 0$, so there is no limit to the amount of nutrients. The results are seen in figures 5.6, 5.7, and 5.8.

The pattern for Setup 1 with regeneration in Figure 5.6 is similar to the pattern without regeneration in 5.3. The difference is that the regeneration case contains regions of high particle concentration and low particle concentration. The nutrient plot shows that where the particle concentration is low, the nutrient concentration is low. What probably causes this unevenness in the concentration of the particles is that in spots with a lot of particles, the nutrients won't grow as much as in spots with few particles. This causes a difference in nutrient concentration. This causes particles to migrate from regions of low nutrient concentration to regions of high nutrient concentration. This again causes a difference in the growth rate of the nutrients. So, the process repeats.

For Setup 2 in figure 5.7 this process also occurs. Unlike the case without the regeneration of nutrients, there is a stripe pattern. The reason for this could be that the particles get closer. This enables the connection between the clusters. Setup 3 with nutrient regeneration in figure 5.8 is similar to the case without nutrient regeneration. There is a large spot with a lower concentration of nutrients. Unlike the case without regeneration, there seems to be no trails behind the clusters where the

v_0	α	D_n	k	D_c	E	a
0.1	0.5	$1000\Delta t$	$1000\Delta t$	$100\Delta t$	$1\Delta t$	$100\Delta t$

Table 5.3: Parameters for Setup 2. These parameters give rise to a dot pattern in the case with no nutrient growth and a stripe pattern when there is nutrient growth.

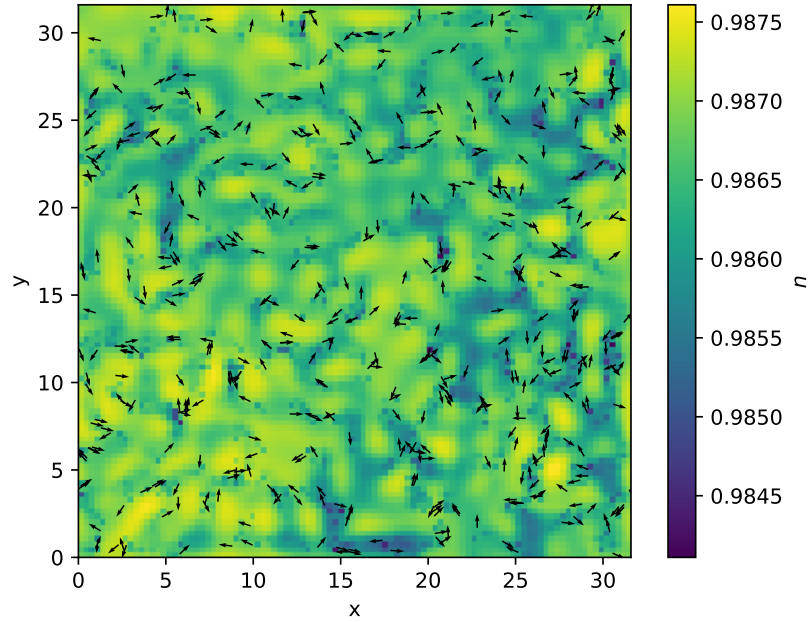
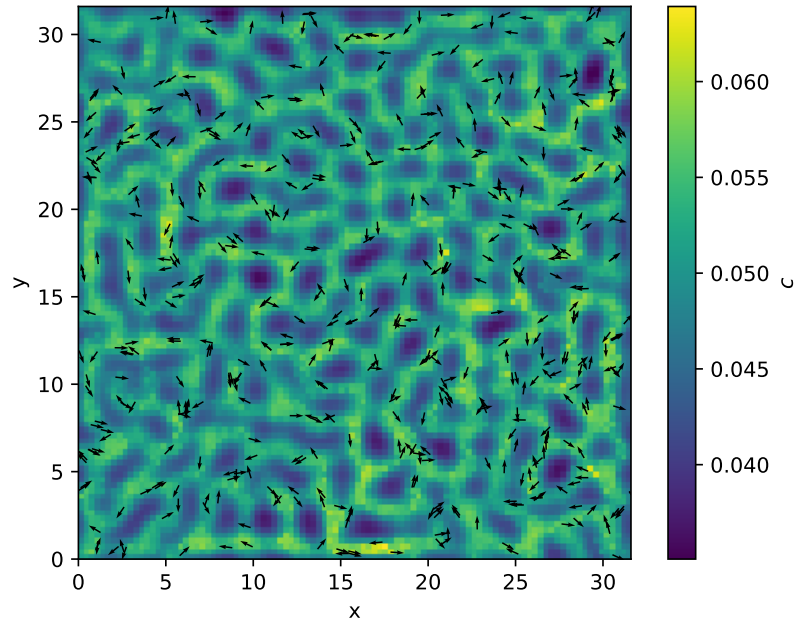


Figure 5.3: Setup 1 without nutrient growth gives rise to a stripe pattern. The plots show the concentrations of nutrients and chemical signals at $t = 999$. The arrows represent the particles, and their directions indicate the particles' headings.

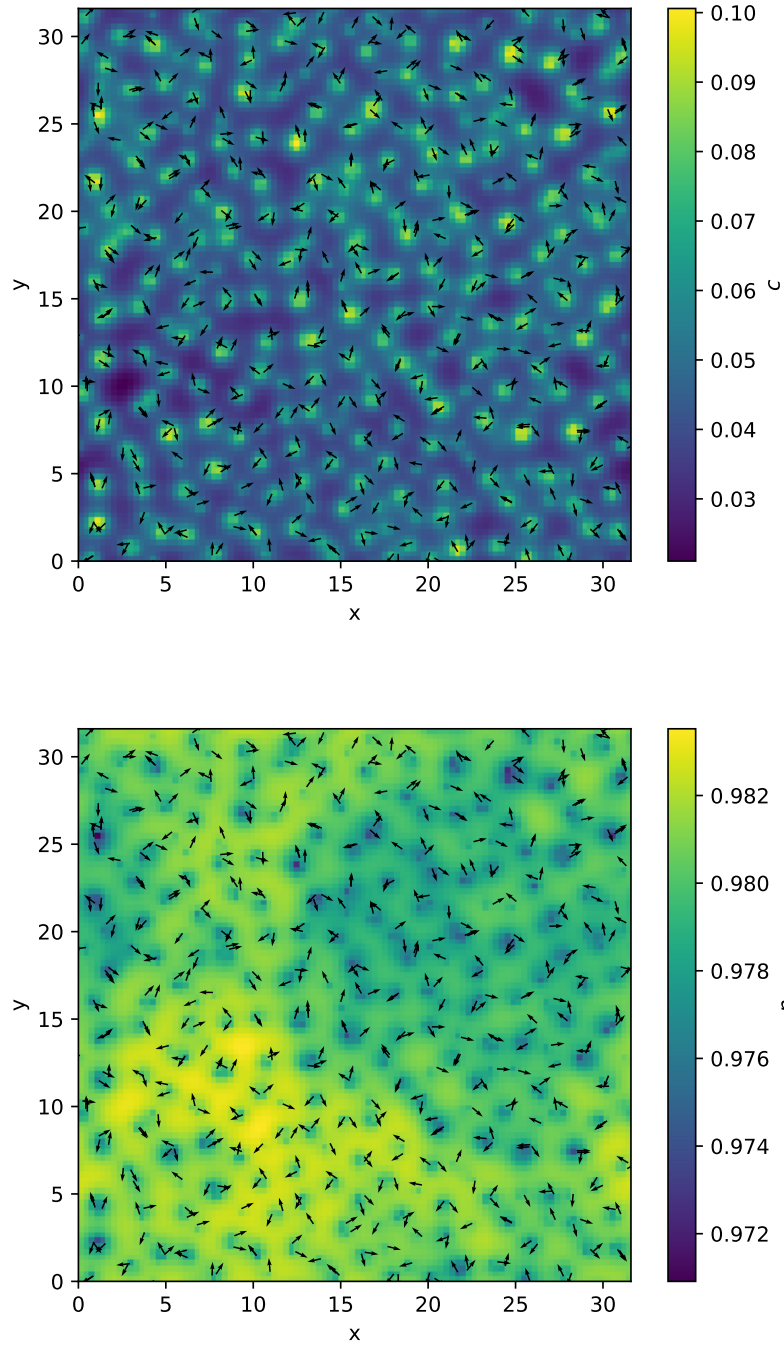


Figure 5.4: Setup 2 without nutrient growth gives rise to dots. The plots show the concentrations of nutrients and chemical signals at $t = 999$. The arrows represent the particles, and their directions indicate the particles' headings.

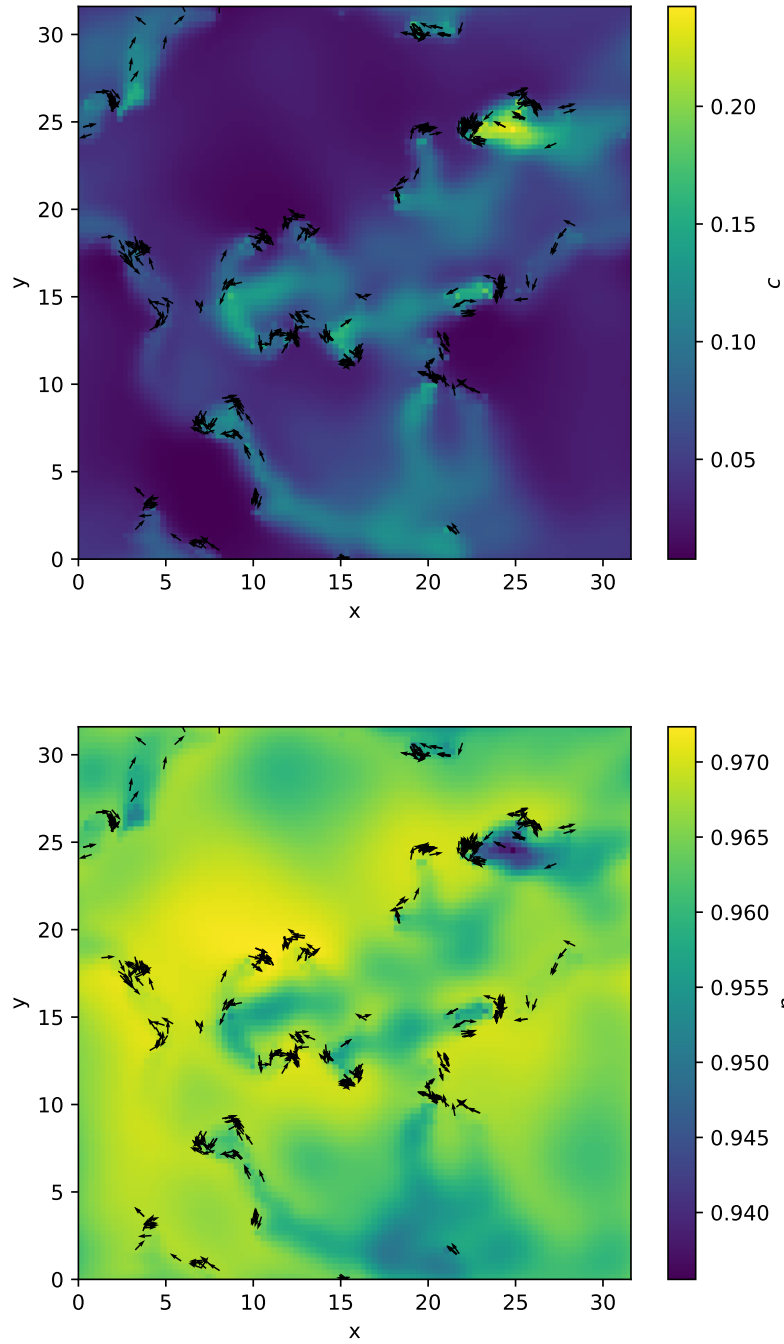


Figure 5.5: Setup 3 without nutrient growth gives rise to moving clusters. The plots show the concentrations of nutrients and chemical signals at $t = 999$. The arrows represent the particles, and their directions indicate the particles' headings.

v_0	α	D_n	k	D_c	E	a
0.5	0.5	$1000\Delta t$	$1000\Delta t$	$1000\Delta t$	$1000\Delta t$	$1000\Delta t$

Table 5.4: Parameters for Setup 3. These parameters give rise to moving clusters.

v_0	α	D_n	k	D_c	E	a
0.1	0.5	$1000\Delta t$	$1000\Delta t$	$100\Delta t$	$100\Delta t$	$100\Delta t$

Table 5.5: Setup used with initial distribution being a Gaussian.

nutrient concentration is low. What probably happens is that the nutrient concentration grows back almost immediately after it has been consumed. Therefore, there are no trails in the nutrient concentration.

5.3.2 Initial nutrient concentration is Gaussian

It will now be shown, what happens when there is a different initial nutrient condition. The initial nutrient will now be Gaussian, which is defined accordingly:

$$g(\vec{r}, \sigma, A) = Ae^{-\frac{\|\vec{r}\|^2}{2\sigma^2}} \quad (5.34)$$

Here σ represents the width. And the maximum is A .

I have used the following initial condition with no regenerations of nutrients:

$$n(r, 0) = g(r - r_c, 1, 1) \quad (5.35)$$

Here, the center of the Gaussian is:

$$r_c = [\frac{L}{2}, \frac{L}{2}] \quad (5.36)$$

The parameters used are in table 5.5. The result can be seen in Figure 5.9.

In the beginning, many particles gather at the center of the Gaussian. They leave trails when traveling there. After some time, the nutrients here get consumed. This causes the organisms to move outward from the center. They tend to move outward along the previously made trails. This makes the chemical signal concentration on the trails larger.

I have tried the same simulations with $v_0 = 1$. The result can be seen in Figure 5.10. Here, the particles do not form trails. Instead, the particles gather at the center of the Gaussian. After the nutrients have been consumed, the particles form an expanding ring. The absence of trails may be due to the particles leaving them immediately after they begin to form.

I have conducted a simulation where the setup was the same, but the initial nutrient concentration was:

$$n(r, 0) = g(r - r_c - \frac{d}{2}\hat{x}, 1, 1) + g(r - r_c + \frac{d}{2}\hat{x}, 1, 1) \quad (5.37)$$

This is a sum of two Gaussians that are a distance d apart. $\hat{x}$ Denotes the unit vector in the x direction. I have used $d = 10$.

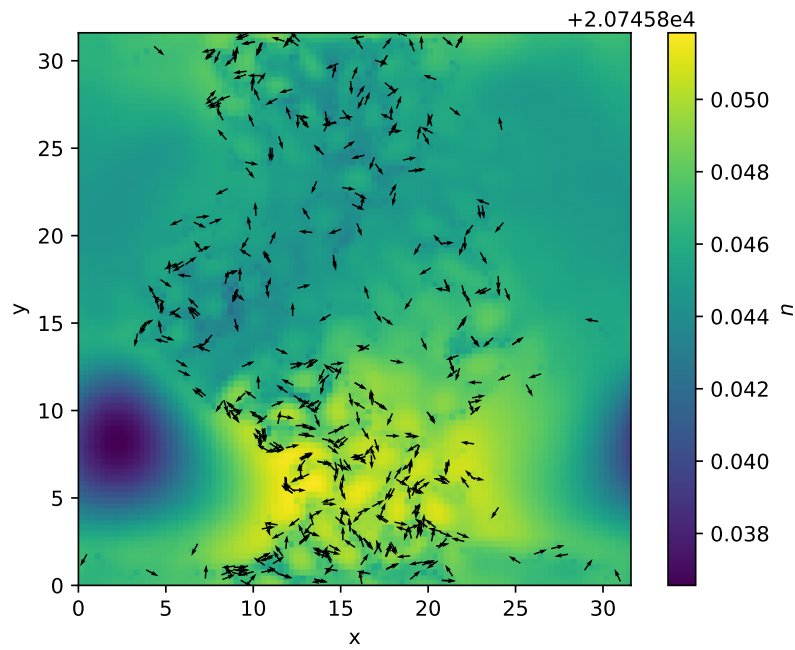
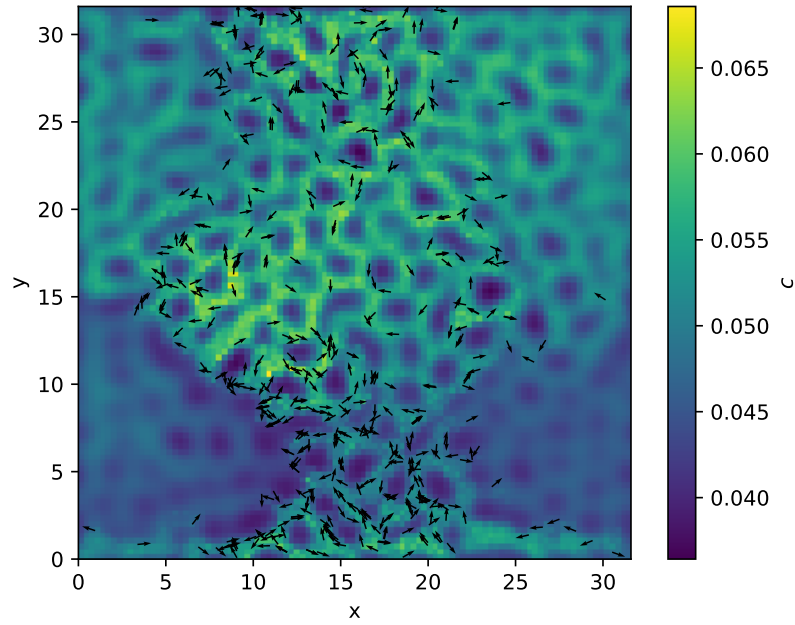


Figure 5.6: Setup 1 with nutrient growth gives rise to a stripe pattern that has spots that are nearly devoid of particles. The plots show the concentrations of nutrients and chemical signals at $t = 999$. The arrows represent the particles, and their directions indicate the particles' headings.

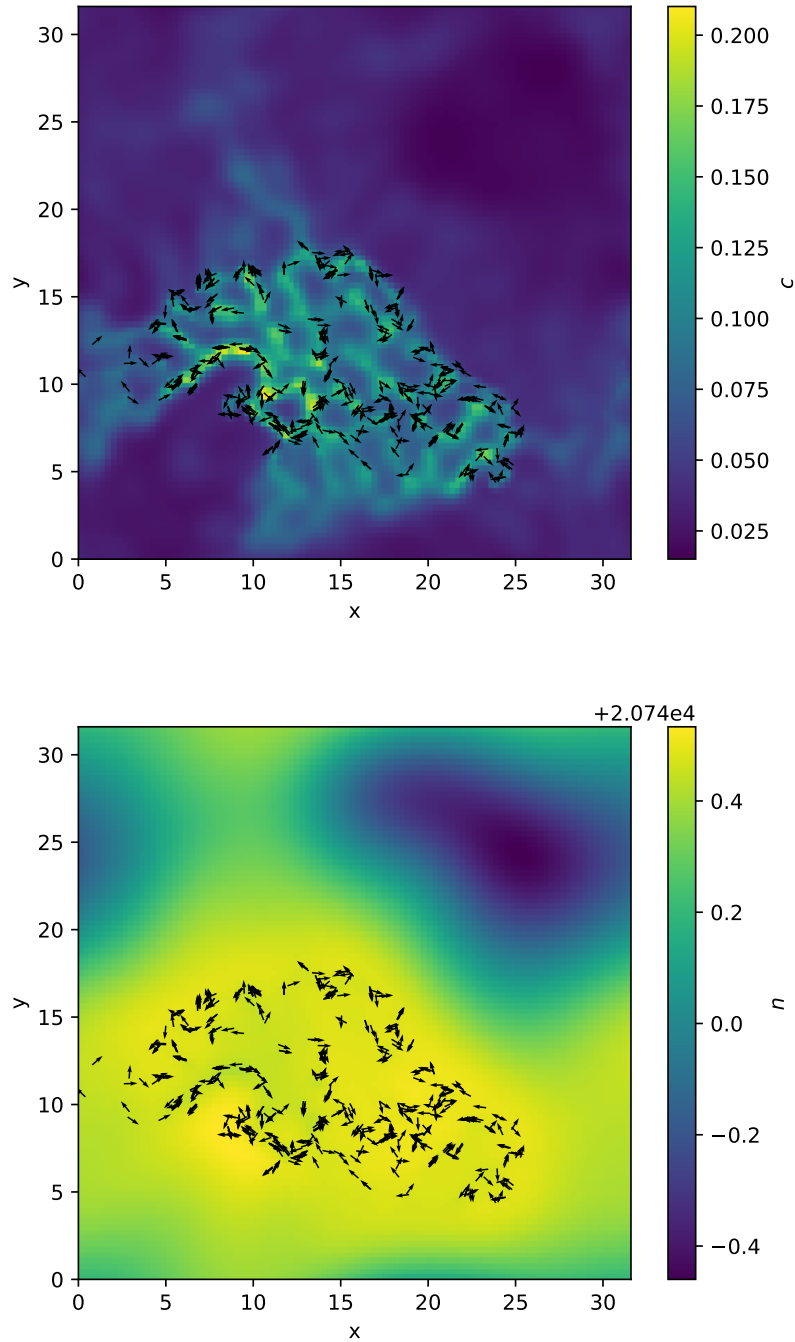


Figure 5.7: Setup 2 with nutrient growth gives rise to a stripe pattern in one spot. The plots show the concentrations of nutrients and chemical signals at $t = 999$. The arrows represent the particles, and their directions indicate the particles' headings.

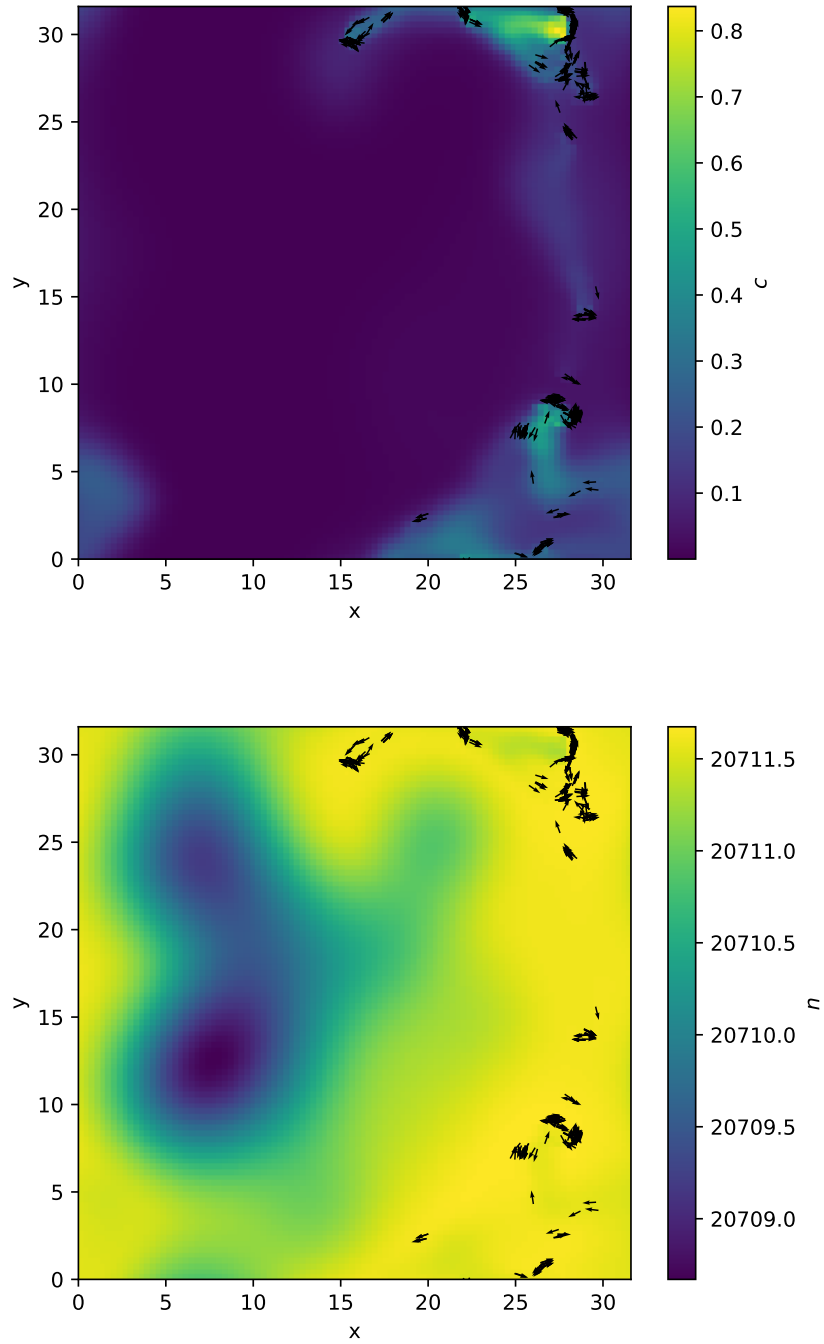


Figure 5.8: Setup 3 with nutrient growth gives rise to moving clusters with no nutrient trails. The plots show the concentrations of nutrients and chemical signals at $t = 999$. The arrows represent the particles, and their directions indicate the particles' headings.

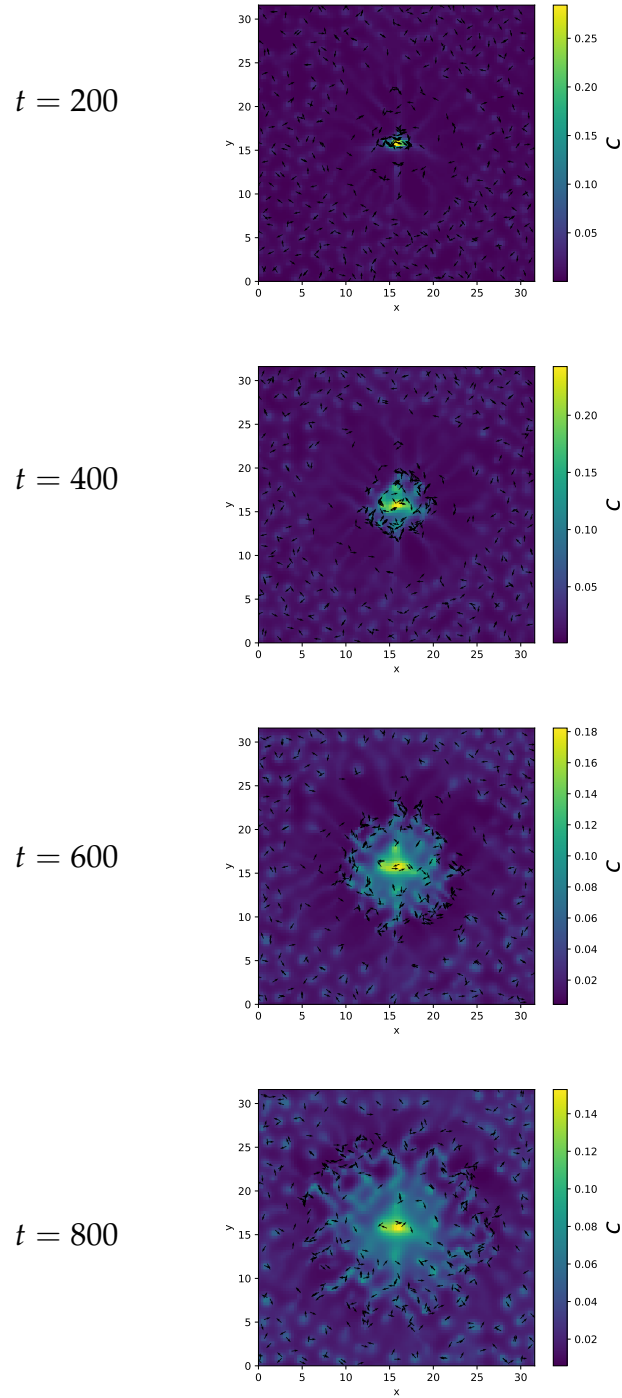


Figure 5.9: Time evolution of particles with low v_0 in the presence of a dynamic chemical signal, starting from an initial Gaussian nutrient concentration. Initially, particles accumulate near the center, followed by an outward migration over time.

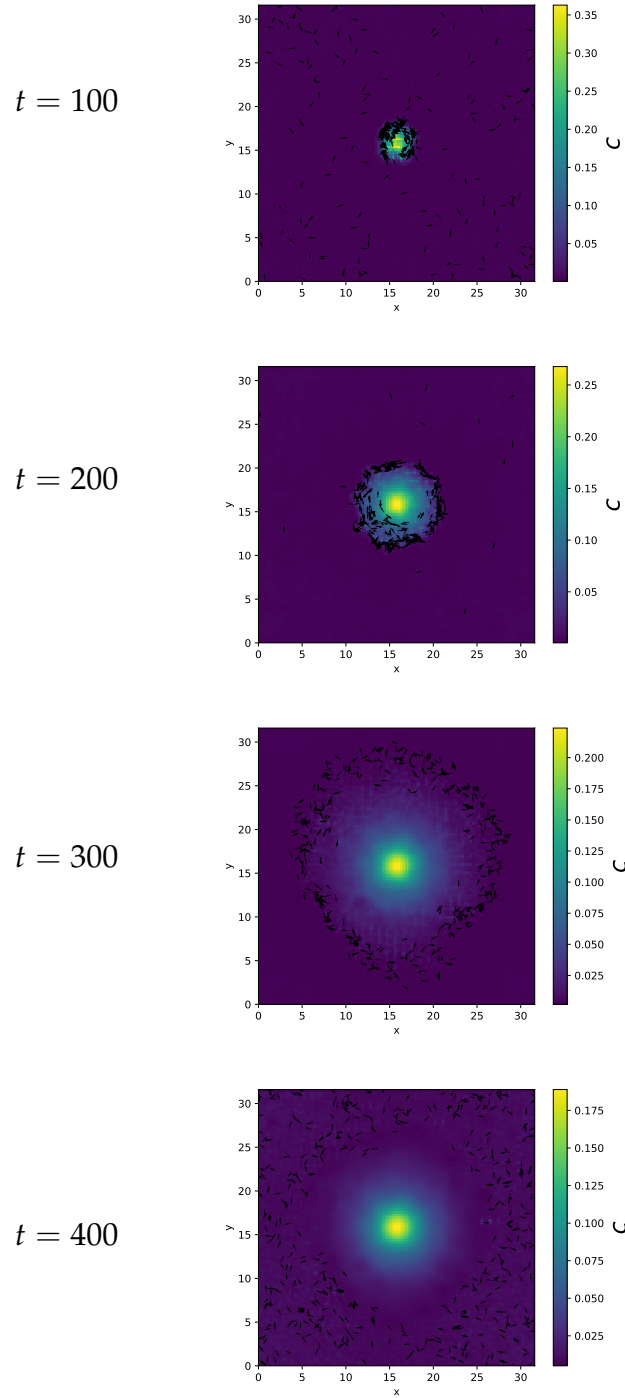


Figure 5.10: Time evolution of particles with high v_0 in the presence of a dynamic chemical signal, starting from an initial Gaussian nutrient concentration. Initially, particles accumulate near the center, then they form an expanding ring as they move outwards.

The results for $v_0 = 0.1$ can be seen in Figure 5.9. The result is similar to the case with the single Gaussian. At $t = 400$ one can see that a trail between the two centers starts forming. After $t = 600$ the centers have been connected. Later, one can see that more trails between them have formed. One can see that the chemical signal concentration is particularly strong along these trails.

I have also done $v_0 = 1$, for the case with two Gaussians. The result can be seen in Figures 5.12. Here, two expanding particle rings form from each Gaussian. The rings eventually merge in the middle, creating a figure eight for a small period. The middle part disappears. This results in an expanding, elongated ring.

5.4 Conclusion

A model for chemotaxis has been presented in which particles move at a constant speed in a direction defined by a linear combination of the nutrient gradient and the chemical signal gradient. The model reproduces characteristic chemotaxis patterns such as stripes and dots. Additionally, under certain conditions, it appears to generate moving clusters. This might help explain why chemotactic organisms such as bacteria sometimes form flocks.

When nutrient growth is present, the system resembles a predator-prey model, with nutrients acting as the prey and particles as the predators. It is well known that a predator-prey system can have oscillations [3]. It has been shown that this chemotaxis model can have regions of relatively low nutrients when nutrient growth is introduced. These spots disappear and appear. This is similar to the variations that can occur in prey population sizes. Most predator-prey models use a varying predator population size. Here, the number of particles is constant. This chemotaxis model may be used for studying the spatial distribution of prey.

Trail patterns have been observed both when the initial nutrient distribution was Gaussian and when it was uniform. These patterns are commonly found in nature. Examples include ant colonies, immune cells [33], and bacteria [4]. As mentioned in the introduction to this thesis, models for collective migration have been used to explain how single cells give rise to multicellular structures. Trail patterns can be seen in multicellular structures. Examples include slime mold[30] and vascular systems. This suggests that this model may be applied to studying the formation of multicellular structures.

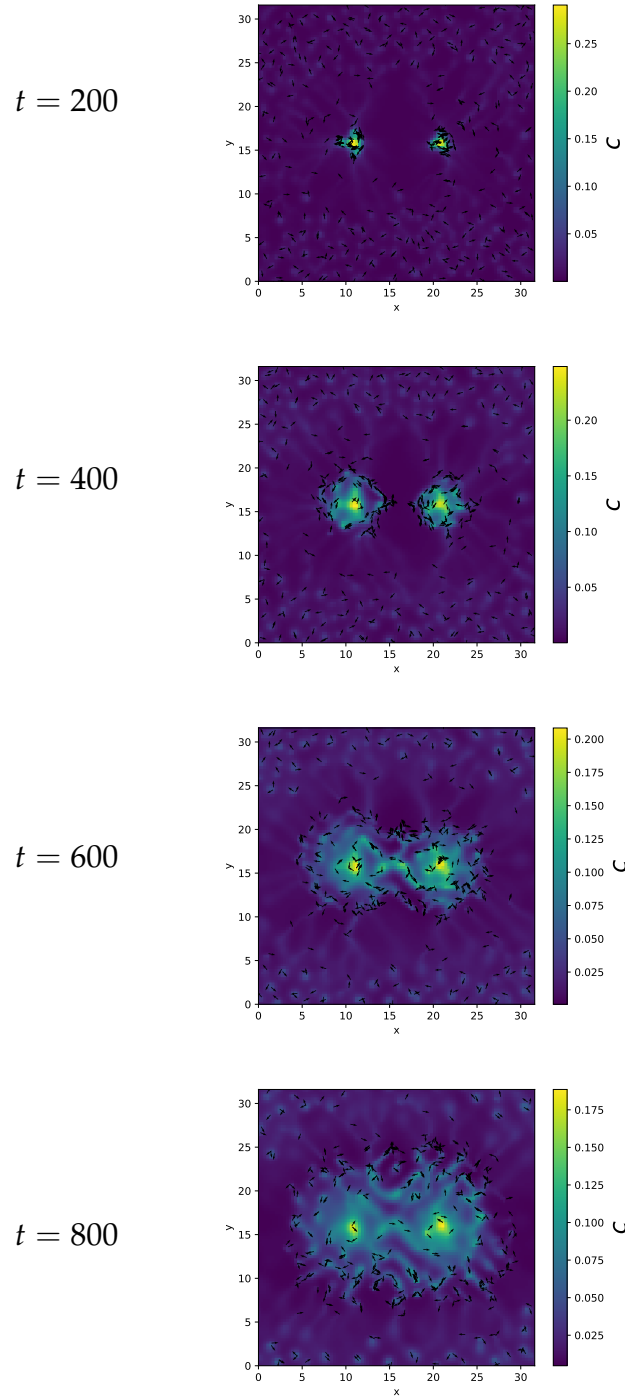


Figure 5.11: Time evolution of particles with low v_0 in the presence of a dynamic chemical signal, starting from an initial nutrient concentration given by the sum of two Gaussian functions. Initially, the particles gather at the centers of the two Gaussian functions. As the particles expand outward, they leave a trail that connects the two centers.

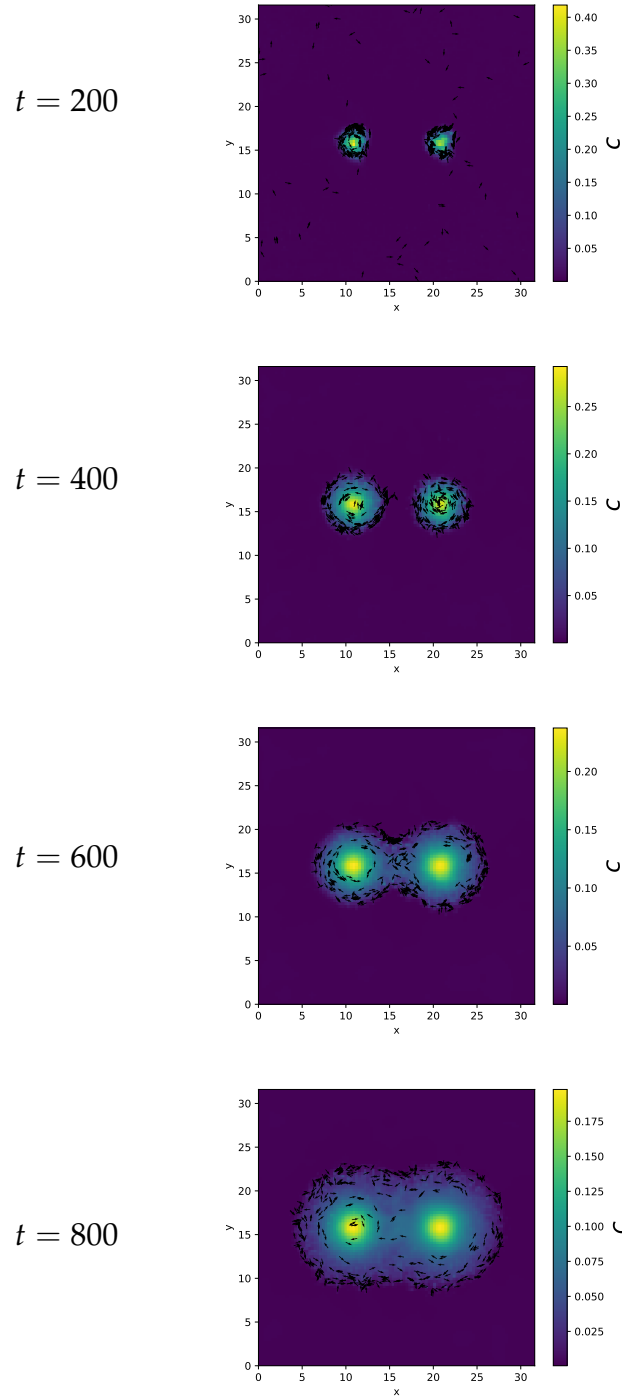


Figure 5.12: Time evolution of particles with high v_0 in the presence of a dynamic chemical signal, starting from an initial nutrient concentration given by the sum of two Gaussian functions. Initially, the particles gather at the centers of the two Gaussian functions. They then end up forming two rings that merge.

Chapter 6

Conclusion and Perspectives

To summarize, I have explored various migration and interaction strategies in binary systems of self-propelled particles. Through numerical study and theoretical considerations, I have explored the direct alignment interactions within two modeling approaches. The first model involved cooperators and defectors: defectors behaved as self-propelled Brownian particles, while cooperators followed the regular Vicsek dynamics. Phase plots that showed when the system ended up with only defectors or only cooperators were shown. These phase plots could potentially be used to explain why flocking evolves or why it does not evolve for some species. This study is a step forward toward a better understanding of cooperative flocking dynamics of biological systems through quantitative models.

In the other model, I considered a system with two particle types. Particles of different types tended to anti-align, while particles of the same type tended to align. The particles also interacted through springs. The model gave rise to rotating clusters with internal structures. The model offers a possible mechanism for how single cells might self-organize into multicellular structures. By interpreting the two particle types as representing distinct cell types, the model could help explain how different cell populations sort themselves into specific spatial arrangements during developmental processes.

Furthermore, I have studied pattern formation and collective behavior due to indirect particle interactions through chemotaxis. I have observed interesting patterns such as stripes, dots, and moving clusters. This model can potentially explain how flocking can emerge due to chemotaxis. The model was able to form trails, which is similar to what ants do.

Future investigations could combine game theory with a chemotaxis model. The model could have cooperators that secrete chemical signals. The defectors would not do this. Each particle would receive a benefit proportional to the chemical signal concentration at its location. Producing the signaling chemical takes energy. Therefore, there would be a cost associated with producing the chemical signal. This system is similar to a Prisoner's Dilemma type game.

An alternative approach would be to consider cooperators that respond to the chemical signal only when its concentration exceeds a given

threshold. Defectors, in contrast, remain unaffected by the signal. The cost of cooperation could then depend on this threshold value. Since the chemical signal becomes stronger as particles come closer together, the threshold effectively defines an interaction radius. In the game theory-based Vicsek model described in this thesis, the cost was proportional to the interaction radius. This formalism can therefore give a chemotactic analogue of the game theory-based Vicsek model.

Game theory could also be coupled with a spring-based model, in which particles are connected by springs that enable cluster formation. The goal of each particle would be to migrate. Clusters would move as a result of the self-propulsion of individual particles. However, only cooperators would actively self-propel, bearing an energetic cost for doing so. This could offer insight into how single cells form multicellular structures.

These approaches together with the models described in this thesis, could help further the understanding of collective motion.

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